# Impacts of alien invasive pine *Pinus radiata* on lizard diversity and thermal habitat quality

by
Elsje Schreuder

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Supervisor: Dr Susana Clusella-Trullas

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## Declaration

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Elsje Schreuder

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## Abstract

Invasive alien plants are responsible for a wide range of changes in native habitats which have cascading effects on the associated native animal communities. Studies of the effects of invasive alien plants on lizard assemblages are limited, especially the effects of Monterey pine, *Pinus radiata*. The objective of this study was to assess the effects of *P. radiata* on lizard assemblages and their associated thermal landscape and prey availability in native mountain fynbos, intermediately invaded fynbos and pine forests, in the Western Cape. Lizards were surveyed in Jonkershoek Nature Reserve and Witzenberg Mountain Range to examine species richness, abundance and diversity. The thermal landscape of each habitat was measured using operative temperature models placed in open and closed canopy sites. Additionally, I examined the availability of prey across habitat types using a range of complementary methods. Lizard species richness, abundance and diversity were greater in the more complex fynbos habitats than in the structurally simpler pine plantations. Along the invasion gradient, semi-invaded fynbos was higher than heavily-invaded fynbos in richness, abundance and diversity of lizards. However, heavily-invaded fynbos had the lowest lizard diversity of all habitat types. Clear differences were shown in habitat structure across all habitat types in both locations, and these directly affected the associated thermal landscape. For both locations, open- and closed-canopy sites in fynbos and intermediately invaded sites represent temperatures targeted by the lizard families found within the Western Cape, providing lizards with the opportunity to thermoregulate. Pine forest open- and closed-canopy sites of both locations rarely reached temperatures that fall within the range of preferred body temperatures typical of these species. Operative temperatures in pine forest habitat were most buffered from temperature variation and had the smallest range of favourable temperatures. Fynbos and intermediately invaded fynbos sites are thermally more heterogeneous than pine forest, presenting lizards with a wider range of basking opportunities. Arthropod abundance and composition followed a similar trend to lizard assemblages, where the quantity and quality of prey varied across habitat types. Pine forest supported the lowest quantity of prey in both locations. This study demonstrates the effects of pine plantations and related invasions on native lizard assemblages and highlights the importance of high quality thermal landscapes to maintain lizard abundance and diversity. I suggest that in areas where *Pinus radiata* is invading native fynbos, lizard assemblages will be disadvantaged by the fast replacement of native habitat with a suboptimal environment composed of altered habitat structure, lowered thermal quality and reduced resources.

## Opsomming

Uitheemse indringerplante is verantwoordelik vir verskeie veranderinge in natuurlike habitatte wat verdere impak op die geassosieerde inheemse diergemeenskappe totgevolg het. Studies oor die effek wat uitheemse indringerplante op akkedis spesiesamestelling het is beperk, veral die effek van Radiataden, *Pinus radiata*. Die doel van die studie was om die effek van *P. radiata* op akkedis spesiesamestelling en die gepaardgaande termiese landskap en beskikbaarheid van prooi in inheemse berg fynbos, fynbos wat intermediêr ingedring word deur dennebome en denneboom woude, in die Wes-Kaap te bepaal. Akkedis-opnames is in beide Jonkershoek Natuurreservaat en die Witzenberg Bergreeks gedoen om spesierykheid, volopheid en diversiteit te ondersoek. Die termiese landskap van elke habitat is gemeet deur middel van operatiewe temperatuur modelle wat in oop en toe blaardak omgewings geplaas is. Verder het ek beskikbaarheid van prooi in die verskillende habitat tipes ondersoek deur die gebruik van ‘n verskeidenheid aanvullende metodes. Akkedis spesierykheid, volopheid en diversiteit was hoër in die meer komplekse fynbos habitat as in die struktureel eenvoudiger denneboom woud. Langs die indringer gradient het fynbos met ‘n lae voorkoms van dennebome ‘n hoër akkedis spesierykheid, volopheid en diversiteit gehad as fynbos met ‘n hoër voorkoms van dennebome. Nietemien, fynbos met ‘n hoër voorkoms van dennebome het die laagste akkedis diversiteit van al die habitat tipes gehad. Daar was duidelike verskille in die habitat struktuur tussen al die habitat tipes, in beide studie areas, en dit het ‘n direkte impak op die termiese landskap gehad. In altwee studie areas het temperature wat in oop en toe blaardak omgewings opgeneem is ‘n reeks temperature verteenwoordig wat deur akkedis families van die Wes-Kaap geteiken word, wat termoregulering geleenthede vir akkedisse bied. Vir altwee studie areas, het oop en toe blaardak omgewings in die denneboom woud selde temperature bereik wat in die reeks van voorkeur ligaamstemperature val tipies vir hierdie spesies. Operatiewe temperature in die denneboom woud was die mees gebuffer, met die kleinste reeks van gunstige temperature. Fynbos en intermediêr ingedringde fynbos was termies meer heterogeen as denneboom woude, wat akkedisse ‘n groter verskeidenheid van bak geleenthede bied. Geleedpotige volopheid en samestelling het n soortgelyke tendens as die akkedis spesiesamestelling gevolg, waar die kwantiteit en kwaliteit van prooi gewissel het oor verskillende habitat tipes. Denneboom woude het die laagste volopheid van prooi in beide studie areas gehad. Hierdie studie toon die effekt van denneboom woude en gepaardgaande indringers op inheemse akkedis spesiesamestellings en beklemtoon die belangrikheid van ‘n hoë kwaliteit termiesie landskap om akkedis volopheid en diversiteit te onderhou. Ek stel voor dat in areas waar *Pinus radiata* besig is om inheemse fynbos in te dring, akkedis

spesiesamestellings benadeel sal word deur die vinnige vervanging van inheemse habitat deur ‘n suboptimale omgewing, saamgestel uit ‘n veranderde habitat struktuur, verlaagde termiesie kwaliteit en verminderde voedsel hulpbronne.

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| | |
|---|---|
| ANOSIM | Analysis of Similarity |
| BG | bare ground |
| CFR | Cape Floristic Region |
| DBH | diameter breast height |
| G | grass |
| IAP | invasive alien plant |
| IT | invasive tree |
| JNR | Jonkershoek Nature Reserve |
| L | logs |
| LLN | native leaf litter |
| LLP | pine leaf litter |
| M | termite mounds |
| NMDS | non-metric multi-dimensional scaling |
| NT | native tree |
| PCA | principal component analysis |
| PT | pine tree |
| R | rocks |
| RDA | redundancy analysis |
| RH | relative humidity |
| S | shrubs |
| T | trunks |
| $T_e$ | operative temperature |
| $T_{sel}$ | preferred body temperature |
| WMR | Witzenberg Mountain Range |

# Chapter 1

## 1.1 General introduction

Invasive alien plants (IAPs) are considered one of the major threats to natural ecosystems at a global scale (Mack *et al*. 2000; Sala *et al*. 2000; Pimentel *et al*. 2005). IAPs can affect composition and habitat structure which in turn affects ecosystem functioning (D'Antonio & Vitousek 1992; Higgins *et al*. 1999) and the diversity of local biota at various scales (Wilcove *et al*. 1998; Mack *et al*. 2000; Gurevitch & Padilla 2004; Ricciardi & Cohen 2007; Pyšek *et al*. 2012). IAPs are important drivers of landscape transformation and contribute to biodiversity loss and homogenization of plant and animal communities (Richardson & van Wilgen 2004; Simberloff *et al*. 2012). IAPs present a serious conservation challenge in the Western Cape Province of South Africa where IAPs occur at a noticeable gradient, particularly in the fynbos biome, where the southern area is highly invaded (Rouget *et al*. 2004; Henderson 2007), 1.6 % of the Cape Floristic Region (CFR) is covered by dense stands of woody alien plants, and a further 30 % of the area is at risk of being heavily-invaded within 20 years (Rouget *et al*. 2004). *Pinus radiata* is considered one of the most widespread and successful invaders in fynbos and is particularly prevalent in mountain fynbos (Richardson *et al*. 1990; Rebelo 1992; Mucina & Rutherford 2007). To date, extensive research has been done on the impacts of IAPs on associated plant communities (Vitousek & Walker 1989; Adair & Groves 1998; Levine *et al*. 2003; Ogle *et al*. 2003; Sax & Gaines 2003; Sax *et al*. 2005; Vilà *et al*. 2006; Hejda *et al*. 2009), but information is lacking on the impacts on animal communities, specifically reptile assemblages (Martin & Murray 2011).

In general, reptiles have specialized habitat requirements (Kanowski *et al*. 2006), are susceptible to habitat modification and face global extinction crises (Gibbon *et al*. 2000). As ectotherms, thermal opportunity and availability are essential to lizards (Dunham *et al*. 1989; Huey 1991) so lizard assemblages are particularly sensitive to changes in habitat structure that alter thermoregulatory opportunities (Attum *et al*. 2006; D'Cruze & Kumar 2011; Pike *et al*. 2011a; Pike *et al*. 2011b; Cosentino *et al*. 2013). Lizards are dominant terrestrial predators and consume a broad range of invertebrates (Pianka 1986; Branch 1998). Therefore, habitat modification could lead to changes in resource availability (Litt *et al*. 2014), which in turn may alter the structure and assemblage of lizard communities. Fynbos is a low shrubby biome in stark contrast to the tall forest created by *P. radiata*. The focus of this project was therefore to investigate the impacts of invasive *P. radiata* on lizard communities inhabiting mountain

fynbos in the Western Cape Province, South Africa, and to test the prediction that *P. radiata* principally alters habitat structure, the thermal landscape and prey availability in the native environment.

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# Chapter 2

## Testing the effects of alien invasive *Pinus radiata* on lizard assemblages in the Western Cape Province, South Africa

## 2.1 Introduction

Given the increasing rate of global change, a primary goal of scientists and conservationists is to improve our assessments of biodiversity and ecosystem function transformation generated by human activities (Tylianakis *et al*. 2008). In the last couple of decades, alien invasive organisms have been considered one of the main drivers of change through the degradation of indigenous habitats (Vitousek *et al*. 1997; Wilcove *et al*. 1998). These changes place biodiversity under great pressure. Invasive alien plants (IAPs) pose a threat to communities by altering processes and properties at the ecosystem-level (Gordon 1998), modifying solar radiation levels (Standish *et al*. 2001), hydrological (Le Maitre *et al*. 1996; Blossey 1999) and nutrient (Vitousek & Walker 1989; Witkowski 1991; Evans *et al*. 2001) cycles, fire regimes (D'Antonio & Vitousek 1992; Rossiter *et al*. 2003) and habitat structure (Ogle *et al*. 2000; Grice 2004). Additionally, IAPs are considered to be responsible for variation in plant community structure and composition, which often results in a lower native plant species richness (Groves and Willis 1999; Higgins *et al*. 1999) and colonization rates (Yurkonis *et al*. 2005), a reduction in native arthropod and vertebrate species richness and abundance (Braithwaite *et al*. 1989; Griffin *et al*. 1989; Herrera & Dudley 2003) and transforming the structure of animal and plant assemblages (Wilson & Belcher 1989). Consequently, the pressures imposed by IAPs raise serious challenges for conserving biodiversity.

Recently Vilà *et al*. (2011) showed that the number of studies undertaken on the impacts of IAPs on animal communities (e.g. species diversity, population dynamics) and, in particular, species performance (growth and fitness) is far less than those that examine the impacts of IAPs on plants. The mechanisms by which the impacts of plant invasions on animal communities take place have been poorly investigated despite the recognition that IAPs have the potential to substantially alter ecosystem structure and function (see review in Levine *et al*. 2003). Furthermore, Martin and Murray (2011) recognized a noteworthy gap in the assessment of and mechanisms underlying the impacts that IAPs have on reptiles and amphibians, which are considered an essential vertebrate group for ecosystem functioning (Pough *et al*. 2004). It is therefore well recognized that such studies are long overdue, especially in regions that have been poorly investigated for such effects.

In South Africa, IAPs not only pose a threat to biodiversity through altering fire regimes, groundwater availability and the rate of nutrient cycling, but also change the functioning of ecosystems by means of creating alterations in plant species composition and through encroachment on native landscapes (reviewed in Richardson & van Wilgen 2004). The Cape

Floristic Region (CFR), located in the south-western region of the Western Cape Province of South Africa, is a globally recognised biodiversity hotspot (Cowling & Pressey 2001), with more than 9000 plant species, of which 69 % are endemic (Goldblatt & Manning 1996; Goldblatt 1997; Linder 2003, 2005). Most of this diversity is associated with fynbos vegetation which is facing major challenges due to the spread of alien trees and shrubs (Richardson *et al*. 1992). According to Richardson *et al*. (1997), mountain fynbos is considered one of the habitats most heavily invaded by IAPs in the Western Cape. However, there are only a few alien tree and shrub species responsible for these severe impacts as these species need resilience to the nutrient-poor soils and frequent fire regimes typical of these areas (Richardson & Cowling 1992). Dense stands of pine trees in the genus *Pinus* are particularly known for altering numerous features in invaded environments (Versfeld & van Wilgen 1986; van Wilgen & Richardson 2012). For example, afforestation by *Pinus* trees and associated invasion in fynbos habitat has caused dramatic loss of plant species diversity (Richardson *et al*. 1992; Holmes & Richardson 1999). Following 35 years of afforestation in fynbos habitat near Stellenbosch, Western Cape Province, a reduction from 75 % to 20 % in native canopy cover, a reduction in the number of native plant species from 298 to 126, and a reduction in mean plant density of 260 to 78 plants $m^{-2}$ were recorded (Richardson & van Wilgen 1986). Therefore, *Pinus radiata* tend to drastically change the landscape in several ways, resulting in a more homogeneous habitat compared to pristine fynbos. Despite numerous studies examining the impacts of invasive pines on native vegetation in this region, the impacts of invasive pine on animal communities and, in particular, reptiles is unknown. Recently, Martin and Murray (2011) reviewed and highlighted three mechanisms by which exotic plants can influence reptile and amphibian species and assemblages. These included changes to habitat structure/heterogeneity, herbivory/predator-prey interactions and reproductive success. Their study provides a novel framework for establishing predictions of the effects of IAPs on reptile and amphibian communities given a set of plant and reptile/amphibian characteristics.

An increase in plant diversity and its associated structural diversity (both temporal and spatial heterogeneity) should result in higher availability of spatial niches, typically increasing the overall amphibian and reptile species richness (Heatwole & Taylor 1987; Duellman & Trueb 1994). Indigenous reptile and small mammal species may rely greatly on microhabitat features such as the percentage leaf litter, woody debris, bare ground, herbaceous plants, shrubs and pine (e.g. Greenberg *et al*. 1994; Flemming & Loveridge 2003; Spencer *et al*. 2005; Kanowski *et al*. 2006; Fischer *et al.* 2004) which provide essential components of the

environment that enhance survival (e.g. shelters, more access to or increased abundance of food, optimal thermal patches for thermoregulation, increased niche partitioning). Therefore, as a result of IAPs, the availability and suitability of spatial niches for animal species may be altered through a change in vegetation composition and habitat structure.

As ectotherms, reptiles rely on their environment to regulate their body temperature for most biological and ecological functions (Heatwole & Taylor 1987). Thermal opportunity and availability is therefore a vital resource for reptiles which can be exploited within a niche, similarly as space or food (Tracy & Christian 1986; van Damme *et al*. 1990). To maintain an optimal range of body temperatures, many reptile species thermoregulate behaviourally by 'shuttling' between sunny and shaded sites or warm and cooler substrates (Heatwole & Taylor 1987; Duellman & Trueb 1994; Shine 1998). A change in vegetation structure due to IAPs could alter the availability of optimal operative temperatures (i.e. 'the steady state temperature of an organism in a particular microclimate in the absence of metabolic heating and evaporative cooling', Angilletta 2009), thus impeding reptiles from maintaining suitable body temperatures, or increasing greatly the costs of doing so. Reductions in thermal opportunity or lack of optimal operative temperatures can have negative effects on the fitness of these organisms (Tracy & Christian 1986; Singh *et al*. 2002). However, the thermal quality of the habitat is highly dependent on the species' body temperature targeted for optimal performance (locomotion, digestion, reproduction) (often approximated by the body temperature selected in a thermal gradient, e.g. Clusella-Trullas *et al*. 2007). Therefore, the consequences of IAPs through this mechanism will be highly dependent on which species are present and their thermal relations. For example, fossorial or burrowing lizard species typically have a lower body temperature preference than rock, ground-dwelling and arboreal species (Greer 1980; Clusella-Trullas *et al*. 2011). Although phenotypic plasticity (e.g. responses to thermal history such as thermal acclimation or seasonal changes in environmental conditions) of performance and optimal temperatures (or $T_{sel}$) has been demonstrated in some cases (Kauffmann & Bennett 1989; Sorci *et al*. 1996; Gvozdík 2012) and reptiles can generally optimize the use of the thermal landscape through behaviour, the thermal adaptation of reptile species forms physiological boundaries that likely impose constraints on the thermal space that species can occupy in altered habitats.

Changes in plant species composition such as those resulting from IAPs can also lead to a reduction in abundance and richness of herbivore insect species (Brandle *et al*. 2008), which will consequently have impacts on insect predators such as reptiles (Herrera & Dudley 2003; Greenwood *et al*. 2004; Martin & Murray 2011). There is great variation in the dietary

preferences amongst reptile species, including herbivores, omnivores and carnivores, although the majority of reptiles prey opportunistically on invertebrates (Heatwole & Taylor 1987; Pough *et al*. 2004; Clusella-Trullas & Botes 2008; Vitt & Pianka 2007). The removal or substitution of food sources, both in abundance and diversity due to habitat alteration, may therefore directly influence the abundance and diversity of reptile species, and possibly most affect those that have specialist diets.

The main objective of the study was to assess differences in lizard species richness and abundance between pine tree-dominated habitats versus native habitats in the Western Cape Province, South Africa. For this, I compared lizard diversity across habitat types and in particular in plots of native mountain fynbos, semi- and heavily-invaded fynbos and pine forest (*Pinus radiata*) at two relatively close locations, Jonkershoek Nature Reserve (JNR) and Witzenberg Mountain Range (WMR). Lizard species richness and abundance are expected to be positively associated with habitat complexity (Figure 2.1a), where fynbos, a highly plant diverse habitat is considered to be more complex than a more homogeneous pine forest typically maintained in plantations. However, lizard species richness and abundance may peak or show intermediate values in intermediately invaded fynbos sites due to increased habitat complexity originating from the mixture of native and alien plants (Figure 2.1b).

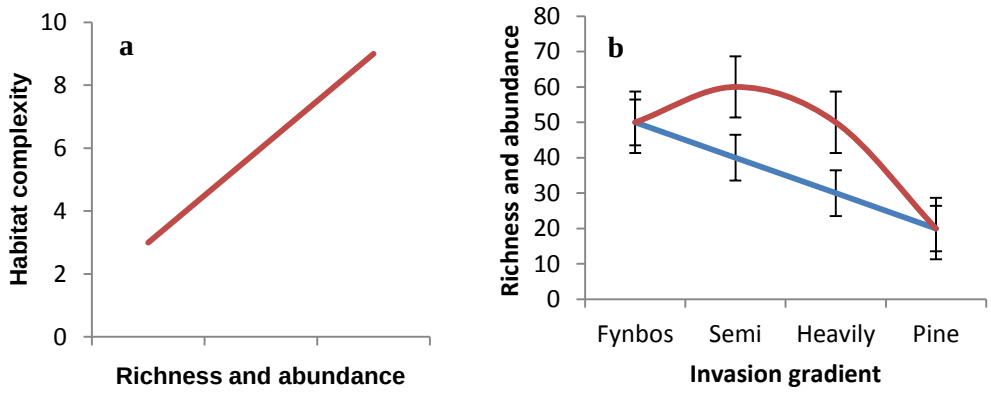


Figure 2.1. Theoretical expectations for the relationships between species richness/abundance and habitat type in this study. In (a), lizard diversity is expected to increase with habitat complexity (with pine forests representing a less complex/heterogeneous habitat compared to fynbos). In (b), at intermediate stages of invasion, lizard diversity and abundance may peak (red) relative to fynbos/pine forests or may decline linearly (blue) from fynbos to pine.

Additionally, I aimed to address two potential mechanisms by which changes in lizard assemblages may occur. Firstly, to assess the thermal quality of each habitat for lizard thermoregulation and secondly, measure resource availability across habitats. I expected that the lowest thermal habitat quality and prey availability would be found in the pine forest. Finally, I aimed to determine whether the differences in lizard species assemblages across habitat types were associated with habitat structure, habitat thermal quality, and resource availability.

## 2.2 Methods

### 2.2.1 Study system background

*Pinus radiata* originates from southwest North America and is an incredibly successful forestry species which has been extensively planted globally. It is considered to pose a fire hazard in fynbos, threatening survival of native animals and plants (The Southern African Plant Invaders Atlas 2006, http://www.agis.agric.za/wip/ accessed 25 September 2014). The "Conservation of Agricultural Resources Act" (Government Gazette 2001) has declared *P. radiata* a category 2 invader, that is, 'an alien invasive species that may be planted for commercial use and only grown in demarcated areas'. This species is considered to be one of the most successful invasive pines in mountain fynbos because its juvenile periods are short, and as an adult, has small seeds with low seed-wing loadings, it is moderately to highly serotinous, and relatively fire-resilient (Richardson *et al.* 1990). The essential features that make *P. radiata* such a successful invader into the fire-prone mountain fynbos include the accumulation of a large seed bank and the tree's dispersal ability (Richardson *et al.* 1990). In South Africa, approximately 340 $km^2$, nearly exclusively in fynbos, has been invaded by *P. radiata* (Macdonald 1991). Native plant species in mountain fynbos communities appear to have a delayed response in the recolonization process during post-fire succession phases (Kruger 1984), which could possibly explain the vast spread of *P. radiata* into mountain fynbos. In contrast, invasion by alien plants is mainly restricted to the immediate post-fire stage (Kruger 1977; Richardson & Brown 1986; Richardson 1988). Richardson and Cowling (1992) have suggested that the success of invaders such as *P. radiata* can be explained by a window of opportunity for germination of these invasive species. More importantly, several authors have suggested that impacts of IAPs are likely to have more severe impacts on native communities in places where the IAP represents a growth form that is absent or minimal in

the invaded community (Martin & Murray 2011). The invasion of *P. radiata* offers such a scenario as mountain fynbos habitats contrast greatly from pine forests, but also, intermediate stages of invasion in the fynbos are readily found.

### 2.2.2 Study sites and lizard sampling

The study was conducted in 2 locations: Jonkershoek Nature Reserve (JNR) (33°59' S, 18°59' E, altitude 427 m asl, aspect: SW, slope: 12-16°) and Witzenberg Mountain Range (private land, WMR) (33°22' S, 19°15' E, altitude 655 m asl, aspect: SW, slope: 20-25°), in the south-western region of the Western Cape Province, South Africa (Figure 2.2.1). These locations were specifically chosen because they encompass plantations of the pine *Pinus radiata* that are adjacent to native mountain fynbos habitat (classification from Mucina & Rutherford 2006). In addition, fires have not occurred in either location for ≥ 6 years. The pine forest in JNR (*ca*. *1*8 km$^2$) is an operating plantation and the forest stand (*ca*. 3 km$^2$) used in this study is *ca*. 15 years old. The pine forest in WMR (*ca*. 16 km$^2$) is 10 years old but has been unmanaged since 2005, thus the habitat structure differs from JNR pine in terms of the amount of uncleared understory present in WMR. In addition, preliminary data on pine characteristics (diameter and height, crown depth and width and tree density) indicated that there were substantial differences between JNR and WMR locations (Appendix C, Figure 3), and therefore, all variables examined in this study were kept separate for the two locations in all analyses. In the WMR location, additional sites were located in semi- and heavily-invaded fynbos vegetation (Figure 2.2.2 and Figure 2.2.3) to reflect the invasion gradient. Unfortunately, these types of sites could not be sampled in JNR because pine is closely monitored and young saplings are readily removed in areas surrounding the pine plantation.

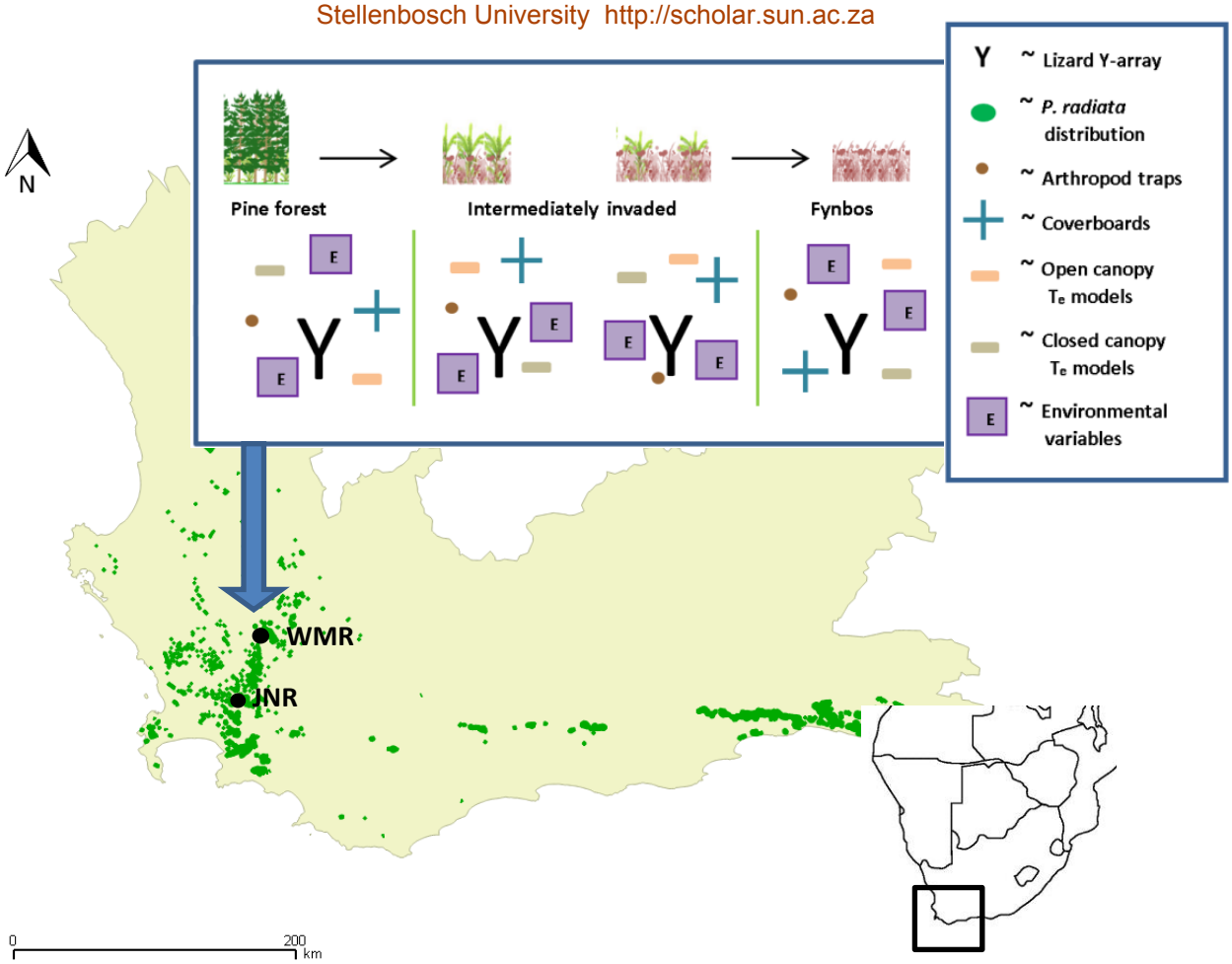


Figure 2.2.1. Sampling replicate design for each habitat type within Jonkershoek Nature Reserve (JNR) and Witzenberg Mountain Range (WMR). The design was repeated 5 times per habitat type.

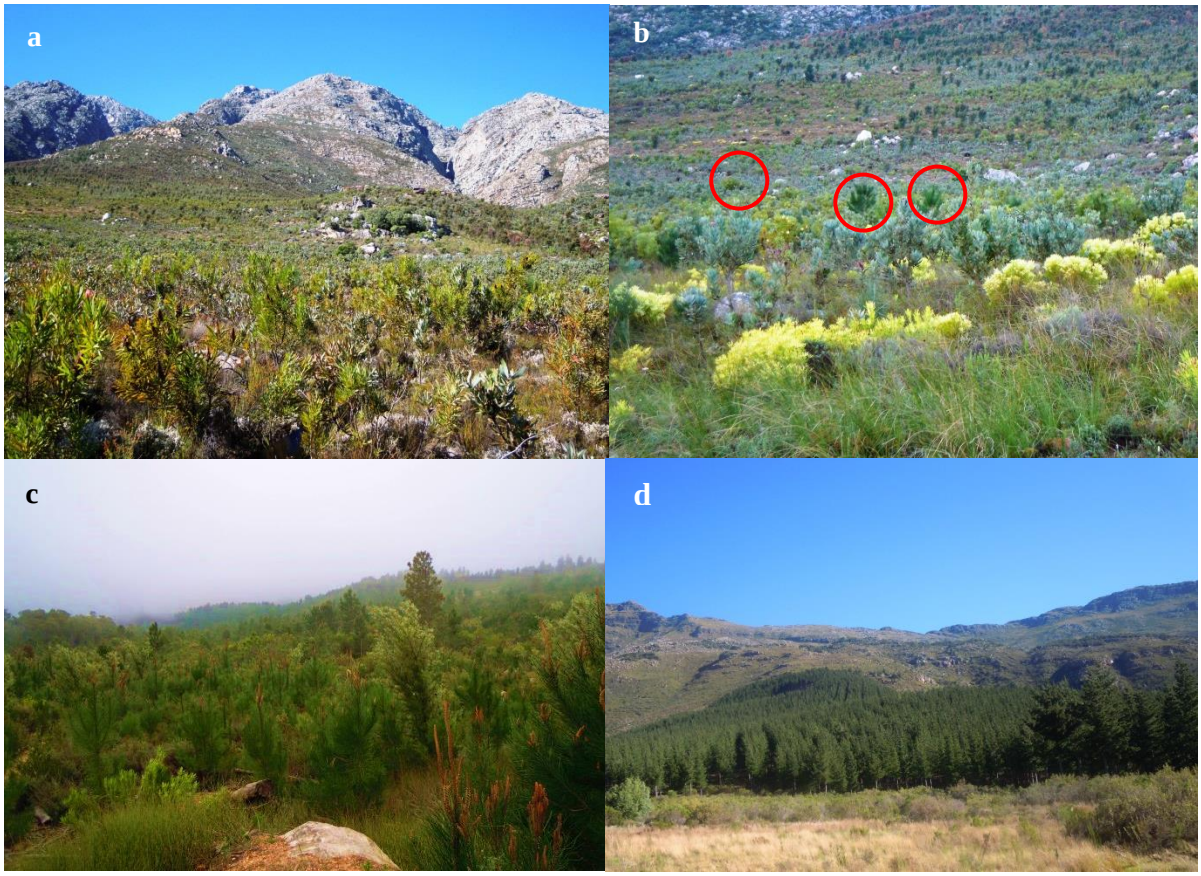


Figure 2.2.2. Habitat types in this study included (a) fynbos: pristine mountain fynbos with no *P. radiata* present, (b) semi-invaded: mountain fynbos with few, generally small *P. radiata* saplings indicated by red circles, (c) heavily-invaded: many and larger *P. radiata* saplings, (d) pine forest: stands of *P. radiata*. Witzenberg Mountain Range sampling encompassed (a) to (d) but only (a) and (d) were present in Jonkershoek Nature Reserve.

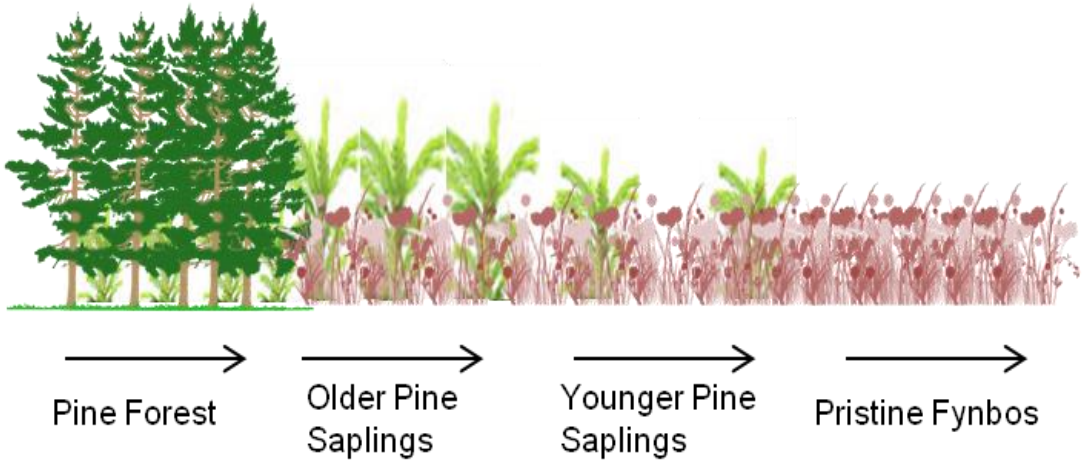


Figure 2.2.3. Succession model of *Pinus radiata* into pristine fynbos, where heavily-invaded fynbos has many and larger *P. radiata* saplings and semi-invaded fynbos has fewer and smaller *P. radiata* saplings.

Five sites were surveyed within each habitat type (fynbos, semi-invaded, pine forest) except for the WMR heavily-invaded fynbos which had three sites due to restricted habitat-type availability. Several sampling techniques were used in each site: one lizard trapping Y-array, active searching and cover boards to capture a good representation of lizard assemblages (Figure 2.2.1; Ribeiro-Júnior *et al*. 2011). Each Y-array consisted of three 15 m arms of 55 cm tall plastic drift fence, buried 10 cm into the ground, spaced at 120° and joined by a central pitfall bucket (10 L). Arms contained two double-ended funnel traps, placed at a point 7.5 m along and on either side of the fence and a pitfall at the end. The funnel traps were sheltered with wooden boards placed diagonally on one side of the trap and moist leaf litter and a wet cloth was placed at the bottom of each bucket to provide protection from predators and direct radiation (additional details on pitfall and funnel traps are given in Appendix A). All the traps were set up one month prior to the start of data collection to prevent confounding effects of disturbance caused by the placement of traps and were checked every 12 hours. Time-constrained active searching was conducted twice a day, at 10h00 and 14h00 by searching natural cover objects such as rocks, logs and leaf litter within each given habitat for 30 minutes. Additionally, during each seven day trapping period, three night searches were conducted at 20h30 by searching the vegetation using a flashlight. Finally, a cross array of 10 artificial wooden coverboards (60 cm x 60 cm x 1.25 cm plywood) positioned 10 m apart were also placed within each site and checked daily.

Traps were situated at least 200 m from the edge of any habitat type as reptile abundance can increase when traps are > 200 m from the edge (Renken *et al*. 2004; Driscoll & Henderson 2008). Each site was sampled for seven consecutive days and separated from each other by 290 m ± 51 m to insure data independence based on small reptile daily movement potential (Heatwole & Taylor 1987). Each site was sampled 11 times during the lizard activity season (from December 2012 to April 2013 and from September 2013 to April 2014, resulting in a total of 43 120 trap nights (with each bucket, funnel and coverboard considered as single traps). Traps were closed between sampling periods and every capture was treated as a new individual unless a recapture occurred within a single seven day trapping period.

Each lizard was identified, photographed and marked with a small dab of water-resistant non-toxic paint to detect recaptures (although rates were low, < 1.7 %). Photographs, voucher specimens and taxonomic keys were used to identify species. Body mass (Precision balance, ML 303E, Mettler Toledo, ± 0.001g), snout vent length and sex were determined before releasing lizards ≥ 15 m from the Y-array when possible.

### 2.2.3. Habitat structure, thermal quality and resource availability

At every site, two 5 $m^2$ quadrats were randomly sampled to record % cover in the following categories: 0-5 %; 6-25 %; 26-50 %, 51-75 %, 76-95 % and 96-100 % for the following habitat categories: tree (native, non-native and pine), shrub, leaf litter (non-native litter (pine and non-pine needles) and native), grass, logs, rocks, bare ground, tree trunks and termite mounds. The habitat structure measurements were repeated four times throughout the study at the same plots (summer 2012, autumn 2013, spring 2013 and autumn 2014).

The range of available operative temperatures ($T_e$) at each habitat type was obtained by using thin hollow copper cylinders (80 x 25 x 15 mm; Shine & Kearney 2001) that resembled an average lizard body size for species found in this region. Temperatures were recorded with an iButton logger (Maxim Thermochron iButtons, DS1922, ± 1.0 °C) placed centrally within each copper model. Ibuttons were suspended in the model hollow cavity to insure insulation from the metal surface (see calibrations in Appendix B). Models were painted with Krylon no. 1318 Grey Primer, Cleveland, Ohio, USA; r = 7.1% which falls within the range of reflectances found among diurnal lizard families in the region (mean reflectance = 12.7 ± 3.8% (range = 5.3 - 17.2 %, see Clusella-Trullas *et al.* 2008). At each site, six models were randomly distributed while ensuring that three models were placed in open canopy sites (typically basking sites) and three in closed canopy sites, resulting in 30 models characterising each habitat type (total of 168 copper models for the study). All models were initially placed at 12h00 to ensure that open and closed canopy sites represented sunny and shaded patches and thus opportunities to thermoregulate. These simple models, despite their potential weaknesses (see Shine & Kearney 2001; Bakken & Angilletta 2014), are adequate for comparing $T_e$ across habitat types. Finally, to incorporate $T_e$ heterogeneity and availability in the landscape, the % of open canopy sites versus closed canopy sites within each site was estimated by quantifying the proportion of sun and shade by measuring sections in each category along a 5m transect, at 12h00 on cloudless days.

In addition, microsite humidity was measured by placing one logger (Maxim Hygrochron iButtons, DS1923, temperature accuracy: ± 0.5 °C) underneath a fine layer (1 cm) of litter or soil material 15 m from two Y-arrays per habitat type. Hygro-buttons were placed in perforated capsules to avoid water saturation. All loggers ($T_e$ and microsite) recorded temperatures hourly from December 2012 to April 2014.

At each site a combination of techniques (pitfall trapping, Berlese-Tullgren funnel litter extractions and bush beating) was used to sample arthropods as it has been shown that a wider

range of species are collected when using different sampling techniques (Olson 1991; Snyder *et al*. 2006). A cross array of 12 pitfall traps (Samways *et al*. 2010) was sampled at each site. The diameter of the pitfall traps was 70 mm, which is small enough to prevent the capturing of vertebrates as by-catches but large enough to effectively capture a wide variety of insects (e.g. Abensperg-Traun & Steven 1995) and spiders (Brennan *et al.* 2005). Each trap was half filled with 70 % EtOH and dishwashing liquid (5 ml; Zytynska *et al*. 2011) and left open for seven days (Borgelt & New 2006). At each site 500 ml of leaf litter was collected and transported to the laboratory within 12 hours of collection. Samples from each site were extracted individually from the litter using Berlese-Tullgren funnel extraction (see Macfayden 1953). Within each site, 10 minutes of bush beating occurred, by placing a 50 $cm^2$ horizontal tray under as many growth forms as possible (bushes, grasses, restios etc.). All pitfall, funnel and bush beating arthropod extractions were stored in 99.9 % EtOH. All samples were processed for identification and abundance counts, insects were identified to family level, and the remaining arthropods were identified to order level, using various taxonomic keys and field guides (Picker *et al*. 2002; Bellinger *et al*. 2014). Arthropods were sampled four times throughout the study (summer 2012, autumn 2013, spring 2013 and autumn 2014).

## 2.3 Analyses

### 2.3.1 Lizard diversity

Species accumulation curves were used to explore the rate at which new species were found and to estimate the expected species richness (Magurran 2004). The cumulative number of species recorded (S) was plotted as a function of sampling effort (number of samples) using the R package vegan (Oksanen *et al*. 2013) ('sample based rarefaction'; Colwell & Coddington 1994; Gotelli & Colwell 2001). Differences in species richness (number of species per survey) and abundance (individuals per survey) across habitat types was first assessed using a Poisson generalized linear model and corrected for overdispersion with a quasi-Poisson distribution (Crawley 2007).

Species richness can be estimated from sample-based species rarefaction curves which preserve the spatial structure of the data by comparison to individual-based rarefaction curves (Magurran 2004; Magurran & McGill 2011). I used five non-parametric richness estimators (Chao 1, Chao 2, Incidence Coverage Estimator (ICE), first and second order Jackknife) to assess species richness per vegetation type, within and across locations (EstimateS V9.1,

Colwell 2009, http://viceroy.eeb.uconn.edu/estimates; Gotelli & Colwell 2001). These indices were chosen as they perform better than extrapolated asymptotic functions and other parametric estimators; they are appropriate for abundance data and are considered to be most accurate given small sample sizes (Hellmann & Fowler 1999; Hortal *et al*. 2006; Magurran & McGill 2011). Asymmetrical 95 % confidence intervals of Chao 1 and Chao 2 were used to assess differences in species richness and abundance among habitat types, with no overlap reflecting significant differences among habitat types (Colwell 2009).

In addition, in order to define species diversity by incorporating both species richness and evenness, Shannon-Wiener's measure of diversity ([ $H' = -\sum_{i=1}^{S} pi \ln pi$] where S is the number of species and *pi* is the proportion of individuals that contribute to the total number of species sampled (Begon *et al*. 1990)) was used to calculate species diversity within each habitat type based on abundance data (Krebs 1989). Combining species richness and evenness can confound patterns (Magurran 2004); therefore I calculated evenness separately using the Shannon evenness index [$E = H'$ / ln(S)], which determines the distribution of species abundances within habitat types. Furthermore, Rényi diversity profiles were calculated to explore the differences in a range of diversity values for each habitat type using the permute (Simpson *et al*. 2014), lattice (Sarkar 2008) and vegan (Oksanen 2013) packages in R. Lizard assemblages can be ranked using Rényi diversity profiles, where an assemblage can be considered more diverse if all of its Rényi diversities are higher than another assemblage (Tóthmérész 1995). Species abundance within locations was assessed using rank abundance curves, which show the proportional contribution each species makes to the total number of individuals observed. Relative dominance was calculated for each habitat type using the Berger-Parker index ([$d = N_{max} / N$], where $N_{max}$ is the number of individuals in the most dominant species and N is the total number of individuals; Berger & Parker 1970) which reflects the pattern seen in the rank abundance curves.

One-way Analysis of Similarity (ANOSIM) using PRIMER6 (Clarke & Gorley 2006) was used to compare community composition across habitats (Clarke & Warwick 2001). Square-root transformed abundance data were used to ensure common and rare species were weighted equally and a pairwise similarity matrix was constructed within each location using a Bray-Curtis similarity measure. The level of difference among habitat types increases as the significant global R statistic approaches one. To compare lizard species richness across habitat types, I repeated the analyses after the data were transformed into presence-absence data. Non-metric multi-dimensional scaling (NMDS) was used to visually display differences in lizard community composition.

### 2.3.2 Differences in microsite temperatures, relative humidity, vegetation structure, and resource availability among habitat types

Hourly temperatures for each copper model recorded during the lizard active period (0700 and 1800, December 2012-April 2013, September 2013-April 2014) were used for $T_e$ data analyses. Daily mean $T_e$s for open and closed canopy microsites were calculated for each model by averaging hourly data across the active season, and then compared across habitat types using a full factorial Analysis of Variance (ANOVA) and Tukey HSD post-hoc tests. The same analysis was undertaken for the absolute maximum and minimum $T_e$ determined for open and closed canopy models. To assess differences in open (or closed) canopy $T_e$ between habitat types, ANOVAs were run separately for each canopy type. To show the effect of time on $T_e$ averaged across the activity season at each hour interval, a repeated-measures ANOVA with hourly mean $T_e$ as the dependent variable and habitat type and time as independent variables was undertaken. To assess variation in temporal $T_e$ distributions, I calculated the average number of hours each copper model required to reach a mean temperature of 31.6 °C. This temperature reflects the mean preferred temperature ($T_{sel}$) of lizard families encountered in the study (i.e. Agamidae, Chamaeleonidae, Cordylidae, Gekkonidae, Gerrhosauridae and Scincidae; 31.6 ± 1.99 °C). Despite being a coarse indicator of targeted temperatures for all species, $T_{sel}$ is typically conserved and varies from 29.3 °C to 35.2 °C across families (Clusella-Trullas *et al*. 2011). For each location, the heating rates among open and closed canopy sites of different habitat types was compared using ANOVAs and Tukey HSD post-hoc tests. Because the distribution of copper models reflected the range of conditions and characteristics of open and closed canopy patches but not their availability in each habitat type, $T_e$ data was weighted using the proportion of open and closed canopy microsites recorded with transects in each habitat. This approach enabled calculation of frequency distributions of available $T_e$s in each habitat type. In order to do this, mean hourly $T_e$ data, from open and closed canopy sites, was randomized to get 100 readings per hour. The percentage of open and closed canopy sites available in a habitat made up the proportion of $T_e$ readings from open and closed canopy sites.

The hourly relative humidity (RH %) measured in leaf litter in each site during the lizard active period (0700 and 1800, December 2012 - April 2013, September 2013 - April 2014) was used for relative humidity data analyses. Hourly mean RH % was calculated for each logger by averaging hourly data across the active season, and then compared across habitat types using a repeated-measures ANOVA with hourly mean RH % as the dependent variable and habitat type and time as independent variables.

A principal component analysis (PCA) was performed to relate a composite of habitat structure variables to habitat type. The main principal components were considered those that had a cumulative variance of more than 80 %. For each site, the average of each habitat structure variable was calculated from two quadrats sampled in each site, resulting in a matrix of 12 variables and 36 sites for JNR and 66 sites for WMR (resulting from the number of sites, habitat types sampled and number of sampling periods: summer 2012, autumn 2013, spring 2013 and autumn 2014). Data were log (x + 1) transformed prior to analyses. The results were displayed using a biplot with scaling set to two to illustrate the correlations between descriptor vectors (correlation biplot) and scaling set to one to illustrate distances among sites (Euclidean distances in multidimensional space).

Arthropod abundance data were obtained by pooling data from all sampling techniques used at each site, also resulting in 36 sites for JNR and 66 sites for WMR (18 samples per habitat type from 4 sampling periods). An ANOSIM was used to compare community composition and the quality of resources (species square-root transformed abundance data and presence/absence data) across habitat types and visualized differences with NMDS.

### 2.3.3. Relating explanatory variables to lizard abundance

A redundancy analysis (RDA) was performed to assess how the combination of environmental variables may explain variation in lizard abundance (Borcard *et al*. 2011; Legendre & Legendre 1998). For each location (JNR and WMR), a species matrix was first constructed by grouping lizard abundances for the 11 lizard sampling surveys by the four environmental survey periods, with two lizard surveys in summer 2012, two lizard surveys in autumn 2013, four lizard surveys in spring 2013 and three lizard surveys in autumn 2014. Additionally, an environmental variable matrix was constructed using variables that were not highly correlated (see correlation matrix, Appendix D) but ensuring that variables for each study dimension (Thermal landscape, Habitat structure, Prey availability and Relative humnidity) were represented in each location (Table 2.3.1). For JNR, the variable ‘Logs’ was not kept in the final model as tree logs only occurred in a single site and were therefore considered to be a poor predictor. The final variables kept for the RDA JNR analysis were min $T_e$, max $T_e$, time, pine tree, prey, and relative humidity. For WMR, RDA analyses incorporated min $T_e$, max $T_e$, pine tree, rocks, native leaf litter, prey and relative humidity. Habitat structure variables were log (x + 1) transformed prior to analyses. The Hellinger transformation was applied to the lizard abundance matrix (Legendre & Gallagher 2001) in

order to use a distance adequate for the study of community composition data incorporating many zeros (Legendre & Legendre 2012; Zuur *et al*. 2007). A backward selection of explanatory variables was conducted to select the 'best' model using the 'step' function in R which utilizes the Akaike's Information Criterion for model choice. The results were visually interpreted using a triplot with scaling set to one (distance triplot) and scaling set to two (correlation triplot). In addition, significance tests based on permutation ('anova' function, with 500 permutations) were used to determine the most significant explanatory variables (Borcard *et al*. 2011; Oksanen *et al*. 2013). Variance partitioning was used (using 'varpart' function in R) to examine the variance explained by sub-sets of explanatory variables (e.g. thermal or habitat structure variables) (Borcard *et al*. 1992; Oksanen *et al*. 2013).

All statistical analyses were conducted in R 3.1.1 (R Development Core Team 2014), PRIMER6 (Clarke & Gorley 2006) and Estimate S (EstimateS V9.1, Colwell 2009, http://viceroy.eeb.uconn.edu/estimates; Gotelli & Colwell 2001). PCA and RDA analyses were undertaken using mass (Venables & Ripley 2002) and vegan (Oksanen *et al*. 2013) packages in R. Additional packages used include lattice (Sarkar 2008) and permute (Simpson 2014) required to run the vegan package.

Table 2.3.1. The study dimensions and variables used in the environmental variable matrix of the redundancy analysis.

| Study dimension | Variable | Definition |
|---|---|---|
| Thermal landscape | Min $T_e$ | Mean of daily min |
| | Max $T_e$ | Mean of daily max |
| | Time | Total number of hours per day in which temperatures within the $T_{sel}$ range were available |
| Habitat structure | PT | Pine tree |
| | NT | Native tree |
| | IT | Invasive tree (other than *P. radiata*) |
| | S | Shrubs |
| | LLP | Leaf litter (pine) |
| | LLN | Leaf litter (native) |
| | G | Grass |
| | R | Rocks |
| | BG | Bare ground |
| | T | Trunks |
| Prey | P | Arthropod abundance |
| Relative humidity | RH | |

## 2.4 Results

### 2.4.1 Lizard diversity

A total of 712 (6 species) and 58 (8 species) individuals were captured for JNR and WMR, respectively (Table 2.4.1). Accumulation curves reached an asymptote for all habitats in JNR and WMR (Appendix D). JNR pine forest had lower species richness (Poisson Generalized Linear Model, z = -4.543, $p < 0.001$; Figure 2.4.1a) and abundance (z = -4.331, $p < 0.001$; Figure 2.4.1b) than fynbos habitat. WMR pine forest and heavily-invaded fynbos had lower species richness (t = -2.324, $p < 0.05$; Figure 2.4.1c) and abundance (t = -2.642, $p < 0.05$; Figure 2.4.1d) than fynbos habitat.

Species richness estimates did not converge in JNR fynbos and pine forest (Figure 2.4.2a and b), nor in WMR fynbos, semi-invaded fynbos, heavily-invaded fynbos and pine forest (Figure 2.4.2c-f) with a difference of 1 species (Mao Tau = 6 species, Jack2 = 7 species) for JNR fynbos, 2 species (Mao Tau = 2 species, Jack2 = 4 species) for JNR pine forest, 11 (Mao Tau = 6 species, ICE = 17 species) for WMR fynbos, 3 (Mao Tau = 4 species, Jack2 = 7 species) for WMR semi-invaded fynbos, 1 (Mau Tau = 2 species, Jack2 = 3 species) for WMR heavily-invaded fynbos and 5 species (Mao Tau = 3 species, ICE = 8 species) for WMR pine forest.

Differences among habitat types in number of species and individuals were supported by non-overlap of 95 % CI of Chao 1 and Chao 2 (Table 2.4.2). For JNR, Chao 1 and Chao 2 were significantly higher in fynbos than pine forest and trend supported by other estimators. For WMR, Chao 1 was significantly higher in fynbos and semi-invaded fynbos than heavily-invaded fynbos (being the less diverse), while Chao 2 was only significantly higher in fynbos than heavily-invaded fynbos. There were no significant differences between pine and any of the other habitat types. Other estimators ranked habitat types variably but consistently ranked species richness highest in fynbos. These patterns are confirmed by Rényi diversity profiles, where all the Rényi diversities are consistently higher in fynbos than other habitat types for both JNR (Figure 2.4.3a and b) and WMR (Figure 2.4.3c-f). Additionally, in WMR, semi-invaded fynbos had higher Rényi diversities than heavily-invaded fynbos and pine forest, with heavily-invaded fynbos having the lowest Rényi diversities. Furthermore, numbers of individuals were most evenly distributed in the pine forest habitat for both JNR and WMR, indicating low levels of dominance by a specific species, whereas in the fynbos habitat species were not evenly distributed indicating high dominance of certain species (Table 2.4.1). Fynbos and pine forest in JNR were mainly dominated by one species as seen in rank

abundance curves (Figure 2.4.4a), where the most abundant species (proportion of total individuals observed within a habitat) was *Agama atra* (56 %) in fynbos, and *Trachylepis homalocephala* (75 %) in pine forest (Table 2.4.1). Similarly, habitat types in WMR were dominated by single species with the exception of the semi-invaded habitat which had 2 species with equal abundances (*Trachylepis homalocephala* and *Trachylepis capensis* (43 % each)) (Figure 2.4.4b). The most abundant species (proportion of total individuals observed within a habitat) were *Trachylepis homalocephala* (47 %), *Tetradactylus seps* (67 %), and *Trachylepis capensis* (50 %) in fynbos, heavily-invaded fynbos and pine forest, respectively.

The ANOSIM of square-root transformed lizard abundance data indicated significant differences in lizard community structure between fynbos and pine in JNR (global R = 1, P = 0.001, number of permutations = 999) (Figure 2.4.5a) and among habitat types in WMR (global R = 0.012, P = 0.006, number of permutations = 999) (Figure 2.4.5c). In WMR, fynbos differed from pine forest and heavily-invaded fynbos significantly (Table 2.4.3). Presence-absence data showed the same patterns: fynbos and pine had significantly different lizard assemblages in JNR (global R = 0.958, P = 0.001, number of permutations = 999) (Figure 2.4.5b) and differences were also apparent in WMR (global R = 0.099, P = 0.001, number of permutations = 999) (Figure 2.4.5d). In WMR, fynbos differed significantly from pine forest and heavily-invaded fynbos (Table 2.4.3).

An ANOSIM of square-root transformed abundance data showed that significant differences were apparent in lizard abundance and presence-absence when comparing fynbos assemblages from both JNR and WMR locations. By contrast, pine forest assemblages did not differ between locations (see Appendix E).

Table 2.4.1. Abundance of lizard species trapped and observed in Jonkershoek Nature Reserve (JNR) and Witzenberg Mountain Range (WMR) across habitat types. F: fynbos; SI: semi-invaded fynbos; HI: heavily-invaded fynbos; P: pine forest.

| Scientific name, common name [a] | F | SI | HI | P | Total |
|---|---|---|---|---|---|
| JNR | | | | | |
| *Agama atra*, southern rock Agama | 395 | 0 | 0 | 0 | 395 |
| *Afrogecko porphyreus*, marbled leaf-toed gecko | 47 | 0 | 0 | 1 | 48 |
| *Cordylus cordylus*, Cape girdled lizard | 152 | 0 | 0 | 0 | 152 |
| *Tetradactylus seps*, short legged seps | 2 | 0 | 0 | 0 | 2 |
| *Trachylepis capensis*, Cape skink | 3 | 0 | 0 | 0 | 3 |
| *Trachylepis homalocephala*, red-sided skink | 109 | 0 | 0 | 3 | 112 |
| WMR | | | | | |
| *Agama atra*, southern rock Agama | 2 | 0 | 0 | 0 | 2 |
| *Bradypodion pumilum*, Cape dwarf chameleon | 1 | 0 | 0 | 0 | 1 |
| *Cordylus cordylus*, Cape girdled lizard | 1 | 0 | 0 | 0 | 1 |
| *Pachydactylus geitje*, ocellated thick-toed gecko | 1 | 0 | 0 | 0 | 1 |
| *Tetradactylus seps*, short legged seps | 5 | 1 | 4 | 2 | 12 |
| *Tetradactylus tetradactylus*, common long tailed seps | 0 | 1 | 0 | 0 | 1 |
| *Trachylepis capensis*, Cape skink | 7 | 6 | 0 | 3 | 16 |
| *Trachylepis homalocephala*, red-sided skink | 15 | 6 | 2 | 1 | 24 |

[a] Scientific and common names follow nomenclature Pyron *et al.* (2013) and Branch (1998).

Table 2.4.2. Observed species richness (sp.) and abundance (Ind.), abundance- and incidence-based richness estimators and Shannon-Wiener diversity (H`), Shannon evenness (E) and Berger-Parker dominance (d) indices for each habitat in Jonkershoek Nature Reserve (JNR) and Witzenberg Mountain Range (WMR). F: fynbos; SI: semi-invaded fynbos; HI: heavily-invaded fynbos; P: pine forest.

| | | | Abundance | | | Incidence | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Sp. | Ind. | Chao1 (95% CI) | Jack1 | Jack2 | Chao2 (95% CI) | ICE | H’ | E | d |
| JNR | | | | | | | | | | |
| F | 6 | 708 | 6 (6.0-8.3) | 6.7 | 7.0 | 6.1 (6.0-9.9) | 6.4 | 1.16 | 0.65 | 0.56 |
| P | 2 | 4 | 2 (2.0-3.7) | 2.9 | 3.7 | 2 (2.0-4.2) | 3.1 | 0.56 | 0.81 | 0.75 |
| WMR | | | | | | | | | | |
| F | 7 | 41 | 10.3 (6.5-45.4) | 9.6 | 12.9 | 11.5 (6.9-41.4) | 16.6 | 1.48 | 0.76 | 0.47 |
| SI | 4 | 13 | 4.9 (4.1-16.4) | 5.8 | 7.5 | 4.9 (4.1-16.2) | 6.4 | 1.10 | 0.79 | 0.43 |
| HI | 2 | 6 | 2 (2.0-3.5) | 2.5 | 2.8 | 2.0 (2.0-4.7) | 2.5 | 0.64 | 0.92 | 0.67 |
| P | 3 | 4 | 3.4 (3.0-10.3) | 4.82 | 6.5 | 3.9 (3.1-15.4) | 7.7 | 1.01 | 0.92 | 0.50 |

Table 2.4.3. WMR analysis of similarity (ANOSIM) results comparing lizard assemblages among habitat types based on Bray-Curtis similarity of square-root transformed abundance data (global R = 0.12, P = 0.006) and presence-absence data (global R = 0.099, P = 0.001).

| | Abundance | | Presence-Absence | |
|---|---|---|---|---|
| Habitat type | R statistic | *P* | R statistic | *P* |
| **Fynbos~Pine** | **0.304** | **< 0.01** | **0.249** | **< 0.01** |
| Fynbos~Semi-invaded | 0.04 | 0.21 | -0.003 | 0.37 |
| **Fynbos~Heavily-invaded** | **0.254** | **< 0.01** | **0.209** | **< 0.05** |
| Pine~Semi-invaded | 0.039 | 0.19 | 0.049 | 0.16 |
| Pine~Heavily-invaded | 0.018 | 0.24 | 0.024 | 0.25 |
| Semi-invaded~Heavily-invaded | 0.061 | 0.10 | 0.064 | 0.12 |

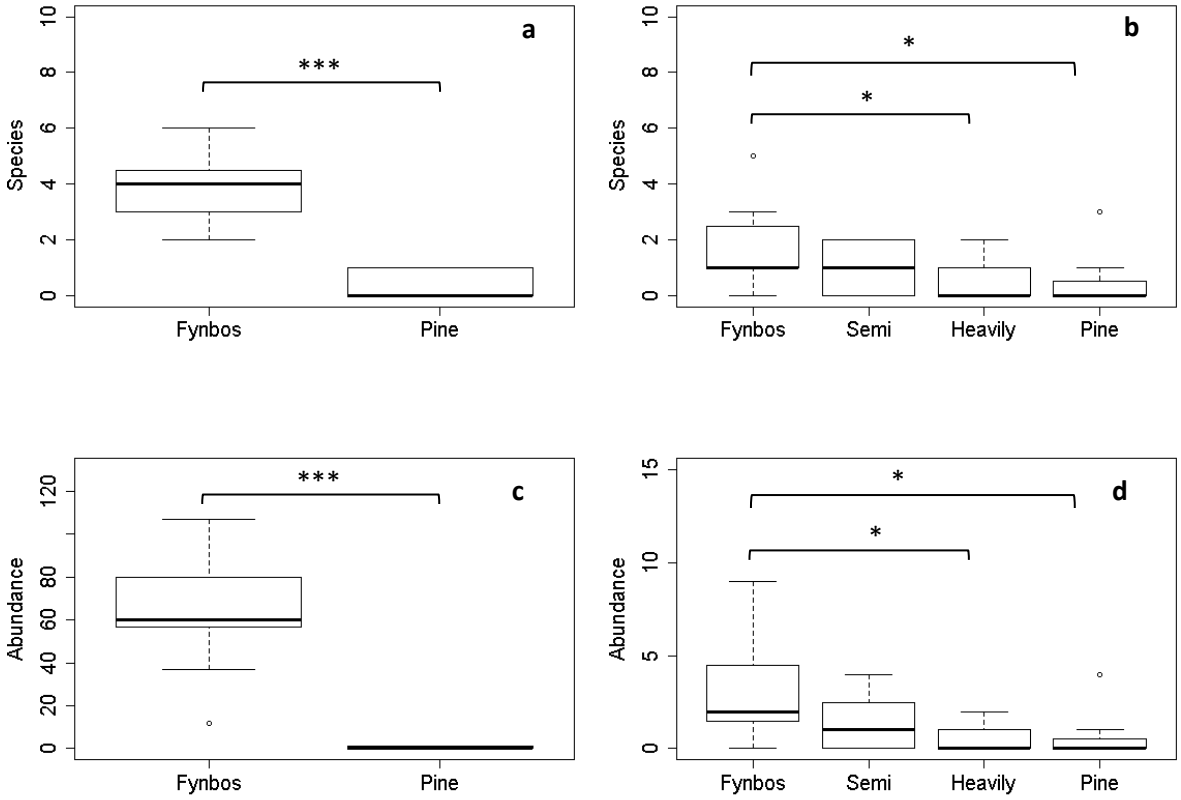


Figure 2.4.1. Number of species per habitat type in JNR (a) and WMR (b), and total number of individuals per habitat type in JNR (c) and WMR (d) for the 11 surveys. Data is pooled for 5 sites within each habitat type. Boxplots represent the median (thicker black horizontal line), inter-quartile range and maximum and minimum values (whiskers). Upper black lines indicate significant differences between habitat types (* = p < 0.05; *** = p < 0.001).

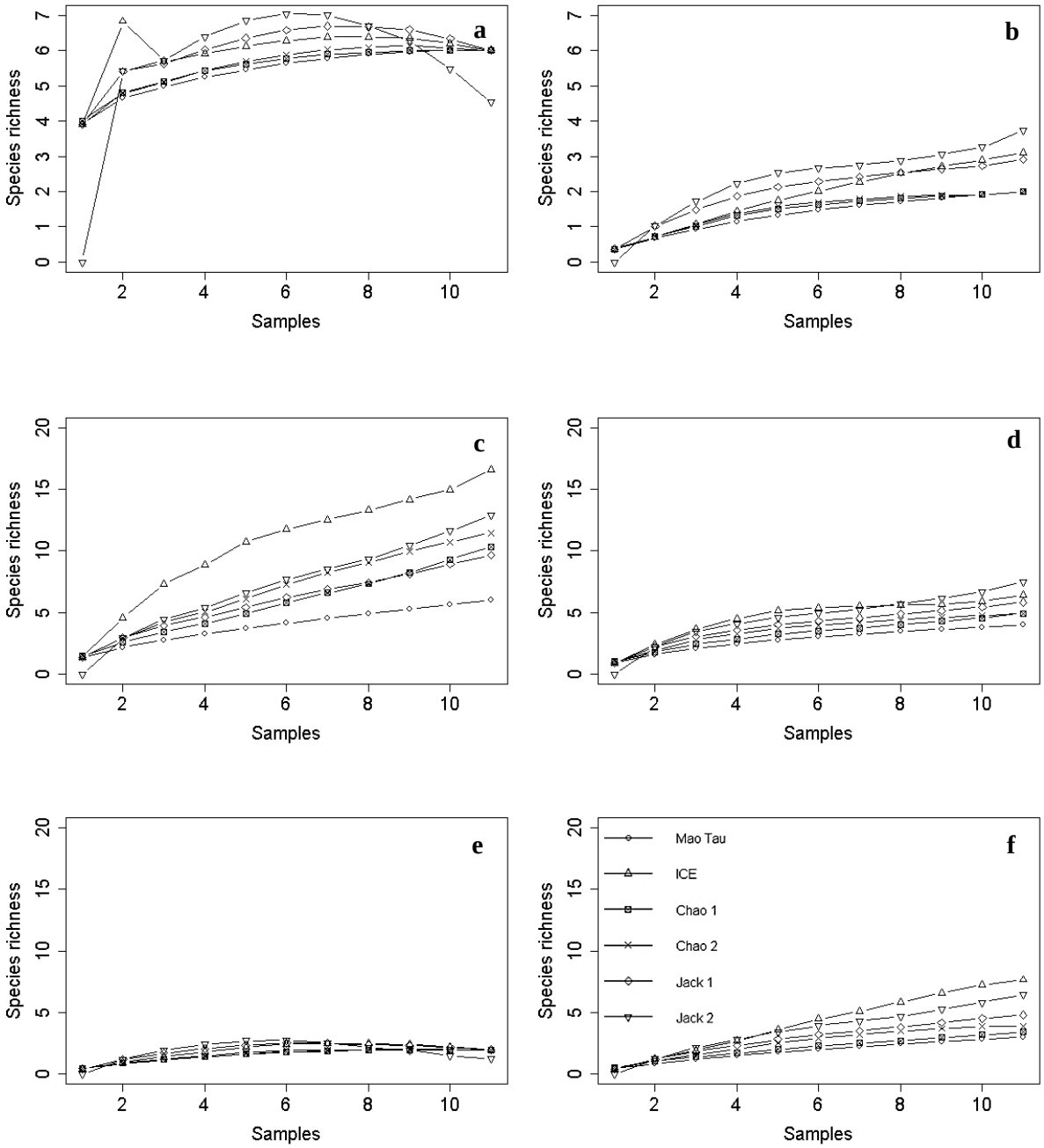


Figure 2.4.2. Species richness estimates (Mao Tau (expected number of species), Incidence Coverage Estimator (ICE); Chao 1, Chao 2, first and second order Jackknife (Jack1, Jack 2)) of JNR fynbos (a) and pine forest (b), and WMR fynbos (c), semi-invaded fynbos (d), heavily-invaded fynbos (e) and pine forest (f).

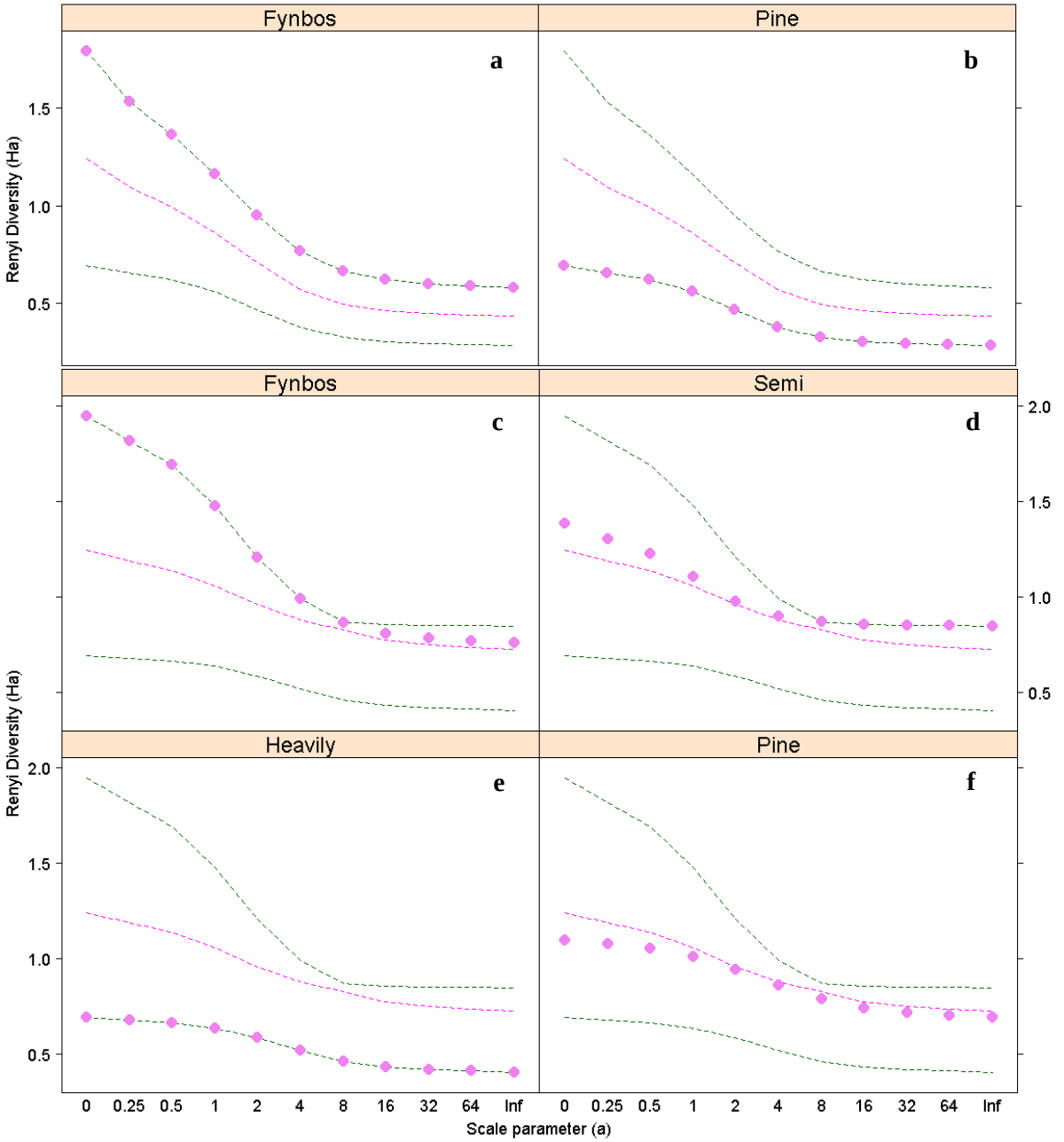


Figure 2.4.3. Rényi profiles of JNR fynbos (a) and pine forest (b), and WMR fynbos (c), semi-invaded fynbos (d), heavily-invaded fynbos (e) and pine forest (f). The diamonds show the values for sites, and the lines are the extremes and median in the data set.

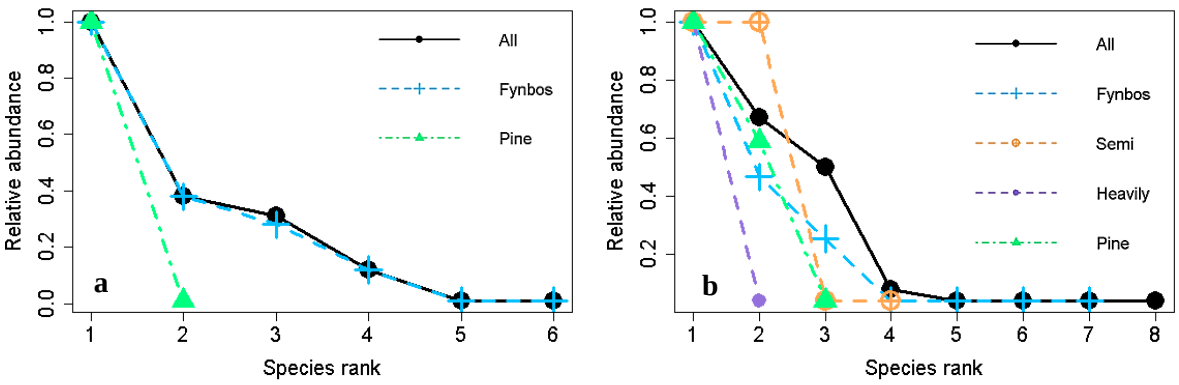


Figure 2.4.4. Rank abundance curves for total number of lizards observed in all sites and different habitat types in JNR (a) and WMR (b).

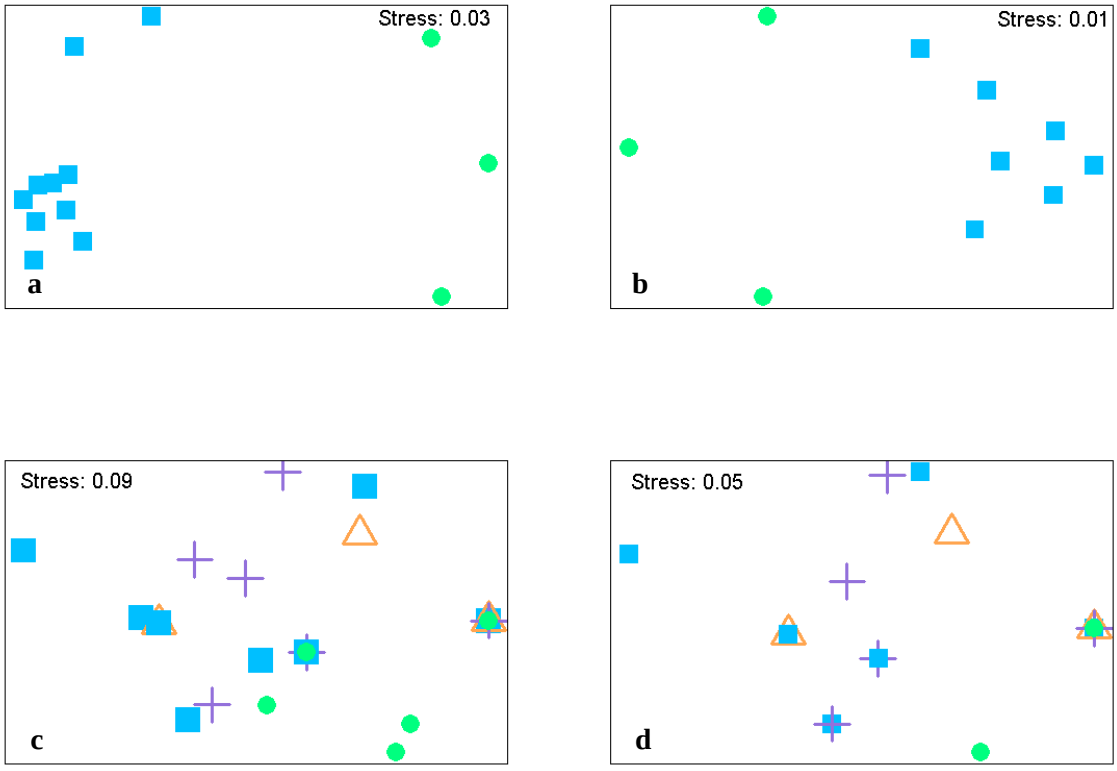


Figure 2.4.5. NMDS ordination of Bray-Curtis similarities based on square-root-transformed lizard abundance data in JNR (a) and WMR (c), and presence/absence data in JNR (b) and WMR (d). Blue squares are samples from fynbos, orange triangles are samples from semi-invaded fynbos, purple crosses are samples from heavily-invaded fynbos and green circles are samples from pine forest. A total of 11 samples per habitat type; due to similarity some are overlaid on top of one another.

### 2.4.2 Differences in microsite temperatures, relative humidity, vegetation structure, and resource availability among habitat types

In JNR, the daily mean and absolute minimum $T_e$ were higher in fynbos than in pine but no significant differences were found in absolute maximum $T_e$ (Table 2.4.4). Open canopy sites had a higher daily mean and absolute maximum $T_e$ than closed canopy sites, but there were no differences in absolute minimum $T_e$ (Table 2.4.4). Significant Habitat x Canopy interactions indicated that the differences between open and closed canopy in daily mean (and absolute minimum) $T_e$ varied depending on habitat type. For open canopy sites, mean and absolute minimum $T_e$ were lower in pine than in fynbos ($F_{1, 28} = 139.3$, $P < 0.001$; $F_{1, 28} = 12.79$, $P < 0.01$, respectively) but there were no differences in absolute maximum $T_e$ ($F_{1, 28} = 1.89$, $P = 0.2$). For closed canopy sites, mean $T_e$ was lower in pine than in fynbos $F_{1, 28} = 6.499$, $P < 0.05$) but there were no significant differences in absolute maximum or minimum $T_e$ ($F_{1, 28} = 1.53$, $P = 0.2$; $F_{1, 28} = 0.06$, $P = 0.8$). For $T_e$ data means, absolute max and min for each canopy and habitat type see Appendix C. Time of day significantly affected mean $T_e$ of open and closed canopy sites (repeated measures ANOVA, $F_{11, 324} = 199.04$, $P < 0.001$, $F_{11, 324} = 43.44$, $P < 0.001$) and the temporal variation of $T_e$ differed between fynbos and pine for open canopy sites (Time x Habitat type interaction, $F_{11, 324} = 4.52$, $P < 0.001$) but not for closed canopy sites ($F_{11, 324} = 0.94$, $P = 0.50$) (see Figure 2.4.6). Fynbos open canopy sites reached mean $T_{sel}$ at a faster rate than pine forest ($F_{1, 28} = 55.56$, $P < 0.001$; Figure 2.4.6a). On average, open canopy sites reached mean $T_{sel}$ (31.6 °C) by ~10h00 (average rate of 4.7 °C per hour), compared to 14h00 in pine forest (average rate of 2.6 °C per hour). Even though fynbos and pine forest closed canopy sites reached a similar max mean $T_e$ at a similar time of the day (~14h00), mean $T_e$ changed at a slightly faster rate in fynbos (2.6 °C per hour) than in pine (1.8 °C per hour; $F_{1, 28} = 14.77$, $P < 0.001$), likely due to fynbos open canopy sites being cooler than pine sites at 07h00 (Figure 2.4.1b). Frequency distributions of $T_e$s weighted by the proportion of available open and closed canopy sites in the landscape showed that fynbos (Figure 2.4.7a) offers a wider range of $T_e$ and higher overlap of $T_e$s with the $T_{sel}$ range compared to the pine habitat (Figure 2.4.7b).

In WMR, the daily mean and absolute maximum $T_e$ in fynbos and semi-invaded fynbos were higher than in pine, and for mean $T_e$, heavily-invaded fynbos was also higher than in pine habitat (Table 2.4.4). By contrast, absolute minimum $T_e$ was higher in pine than in semi-invaded fynbos and fynbos, while no differences were found between pine and heavily-invaded fynbos. Similarly, absolute minimum $T_e$ in heavily-invaded fynbos was higher than semi-invaded fynbos and fynbos (Tukey HSD post-hoc test, all $P < 0.001$). Open canopy sites

had a higher daily mean and absolute max $T_e$ and lower absolute min $T_e$ than closed canopy sites (Table 2.4.4). Patterns of daily mean $T_e$ for open and closed canopy sites differed depending on the habitat (Habitat x Canopy interaction, Table 2.4.4). For open canopy sites, daily mean and absolute max $T_e$ in pine was significantly lower than in any other habitat type ($F_{3, 50} = 70.01$, $P < 0.001$, $F_{3, 50} = 26.5$, $P < 0.001$, respectively). For closed canopy sites, daily mean $T_e$ in pine was also significantly lower than in any other habitat type ($F_{3, 50} = 10.15$, $P < 0.001$) but there were no differences in absolute max $T_e$ across habitats ($F_{1, 50} = 0.849$, $P = 0.5$). For both open and closed canopy sites, heavily-invaded fynbos and pine had higher absolute min $T_e$ than semi-invaded fynbos and fynbos ($F_{3, 50} = 22.35$, $P < 0.001$, $F_{3, 50} = 31.53$, $P < 0.001$, respectively). For $T_e$ data means, absolute max and min for each canopy and habitat type see Appendix C. Time of day significantly affected $T_e$ of open (and closed canopy sites (repeated measures ANOVA, $F_{11, 588} = 204.9$, $P < 0.001$, $F_{11, 588} = 105.3$, $P < 0.001$, respectively) and the temporal variation of $T_e$ differed among habitat types for both open and closed canopy sites (Time x Habitat type interactions, $F_{33, 588} = 8.39$, $P < 0.001$, $F_{33, 588} = 2.49$, $P < 0.001$, respectively) (see figure 2.4.6). In open canopy sites, the rates of $T_e$ change prior to reaching $T_{sel}$ differed across all habitat types (habitat type effect, $F_{3, 50} = 49.66$, $P < 0.001$) with the exception of fynbos and semi-invaded fynbos (post-hoc test, $P > 0.05$) (Figure 2.4.6c). Fynbos and semi-invaded fynbos $T_e$ reached mean $T_{sel}$ by ~11h00 at a faster average rate of increase (5.0 °C and 5.1 °C.hour$^{-1}$, respectively) than heavily-invaded fynbos ($T_{sel}$ at ~12h00, rate of increase of 3.4 °C.hour$^{-1}$) and pine forest (~14h00, 2.2 °C.hour$^{-1}$). For closed canopy sites, the rate of change prior to reach $T_{sel}$ in pine forest was significantly lower than any other habitat (habitat type effect, $F_{3, 50} = 5.41$, $P < 0.001$) (Figure 2.4.6d) but no differences were found between other habitats. Heavily-invaded fynbos reached mean $T_{sel}$ at the fastest rate ~12h00 (3.3 °C.hour$^{-1}$). Semi-invaded fynbos and fynbos $T_e$ reached mean $T_{sel}$ ~13h00 (at 3.1 °C and 3.0 °C per hour, respectively) while $T_e$ in pine forest reached mean $T_{sel}$ at the slowest rate ~13h00 (2.1 °C.hour$^{-1}$). $T_e$ frequency distributions in fynbos, semi- and heavily-invaded fynbos (see figures 2.4.7c-e) that incorporated the availability of both open and closed canopy sites had a broader range and higher overlap with $T_{sel}$ than pine forest (Figure 2.4.7f).

Table. 2.4.4. Full factorial ANOVA for the effect of habitat type and canopy (open and closed canopy sites) on mean, absolute maximum and minimum $T_e$ temperatures for JNR and WMR.

| Location | Temperature | Coefficient | DF | F-value | *p*-value |
|---|---|---|---|---|---|
| JNR | **Mean** | **Habitat** | **1** | **102.05** | **< 0.001** |
| | | **Canopy** | **1** | **115.09** | **< 0.001** |
| | | **Habitat x Canopy** | **1** | **41.89** | **< 0.001** |
| | **Max** | Habitat | 1 | 0.190 | 0.66 |
| | | **Canopy** | **1** | **85.481** | **< 0.001** |
| | | Habitat x Canopy | 1 | 3.029 | 0.09 |
| | **Min** | **Habitat** | **1** | **7.760** | **< 0.01** |
| | | Canopy | 1 | 0.671 | 0.42 |
| | | **Habitat x Canopy** | **1** | **6.042** | **< 0.05** |
| WMR | **Mean** | **Habitat** | **3** | **54.66** | **< 0.001** |
| | | **Canopy** | **1** | **76.74** | **< 0.001** |
| | | **Habitat x Canopy** | **3** | **4.84** | **< 0.01** |
| | **Max** | **Habitat** | **3** | **6.899** | **< 0.001** |
| | | **Canopy** | **1** | **15.406** | **< 0.001** |
| | | Habitat x Canopy | 3 | 2.144 | 0.09 |
| | **Min** | **Habitat** | **3** | **51.015** | **< 0.001** |
| | | **Canopy** | **1** | **45.757** | **< 0.001** |
| | | Habitat x Canopy | 3 | 0.763 | 0.52 |

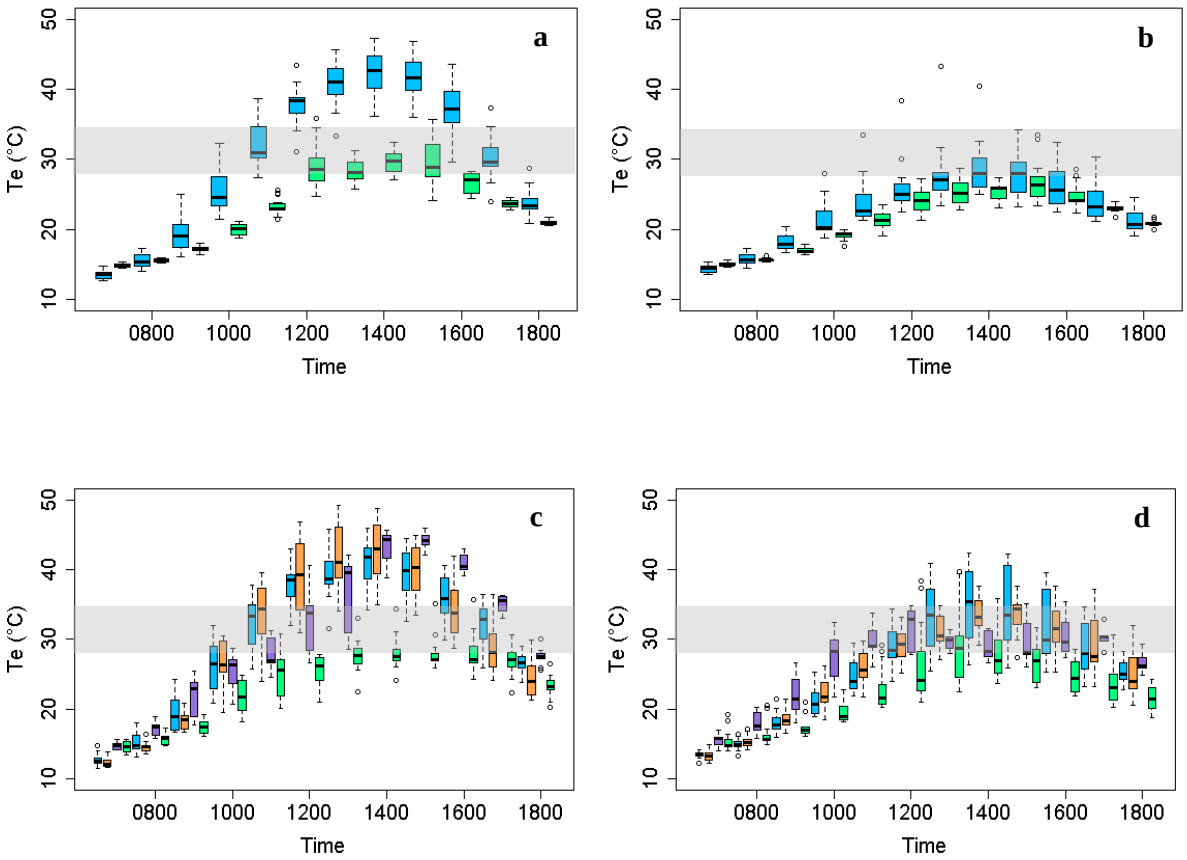


Figure 2.4.6. Operative temperature ($T_e$) in open sites of JNR (a) and WMR (c), and closed canopy sites of JNR (b) and WMR (d) in fynbos (blue), semi-invaded fynbos (orange), heavily-invaded fynbos (purple) and pine forest (green). Boxplots represent the median (thicker black horizontal line), and inter-quartile range with whiskers set at maximum and minimum values for each time of day. Grey shaded bar represents the range of mean $T_{sel}$ of families encountered in this study (data taken from Clusella-Trullas *et al*. 2011).

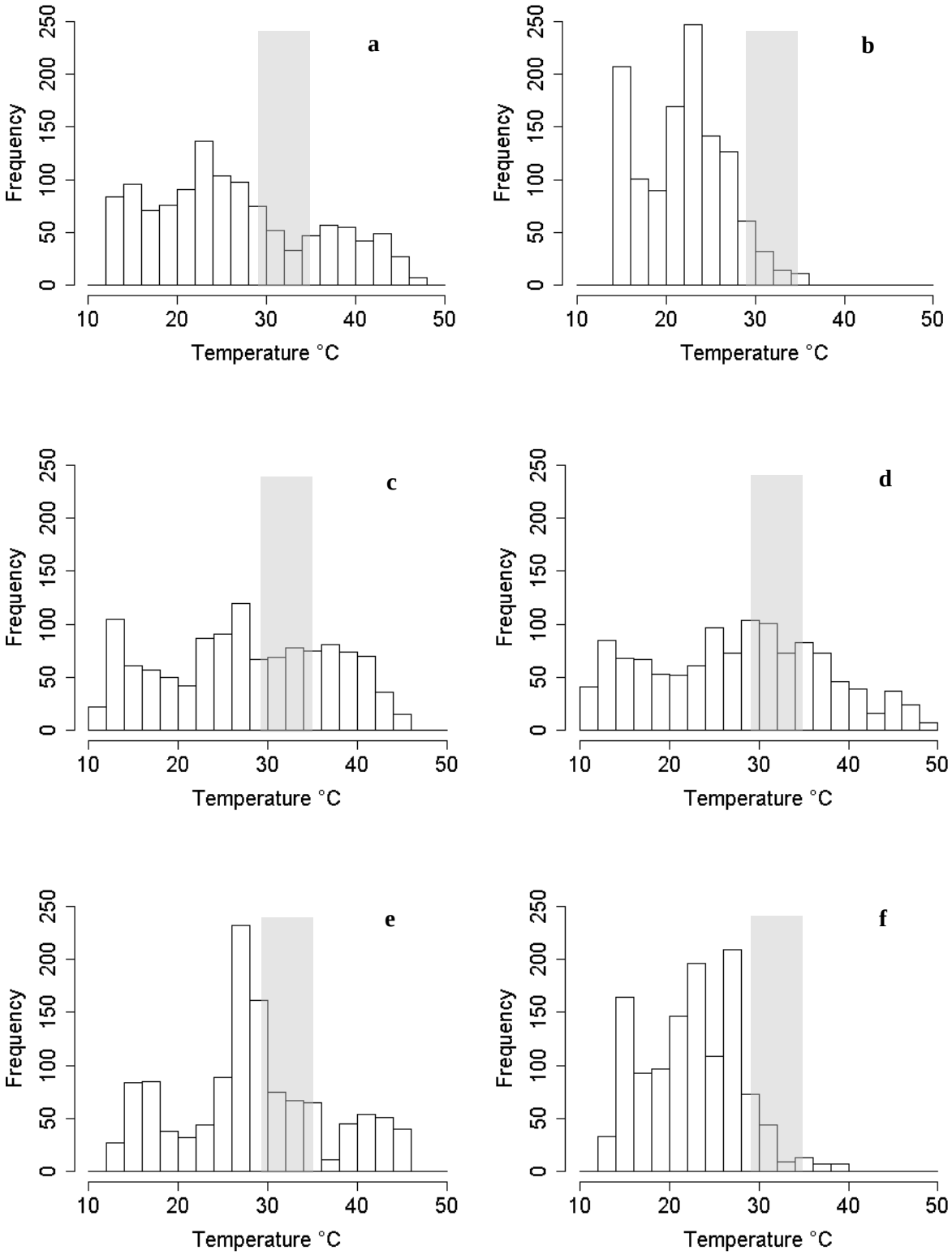


Figure 2.4.7. Weighted frequencies of $T_e$s in open and closed canopy sites of JNR fynbos (a) and pine forest (b), and WMR fynbos (c), semi invaded fynbos (d), heavily-invaded fynbos (e) and pine forest (f). Grey shaded bars represent the range of mean $T_{sel}$ of families encountered in this study (data taken from Clusella-Trullas *et al*. 2011).

In JNR, hourly mean RH % in leaf litter was significantly higher in the pine forest (repeated measures ANOVA, $F_{1, 11} = 9.389$, $P < 0.01$, Figure 2.4.8a), whereas in WMR there were no differences among habitat types (Figure 2.4.8b).

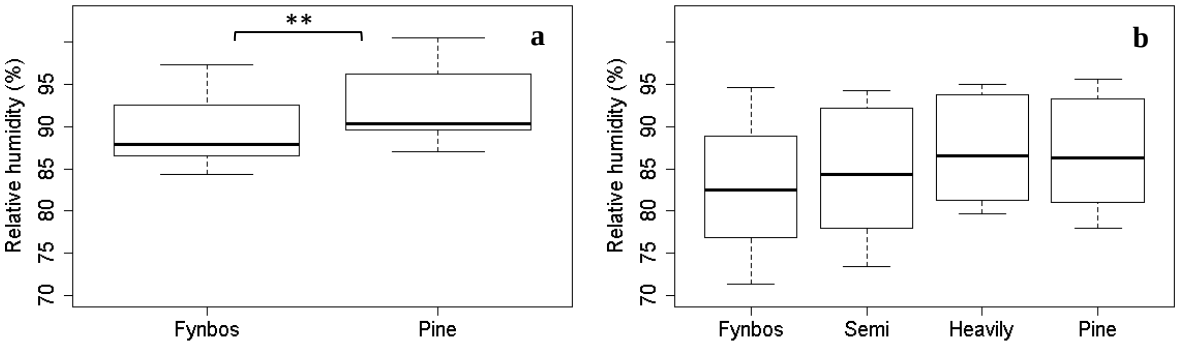


Figure 2.4.8. Range of hourly leaf litter RH % of pine forest habitat was significantly wetter than fynbos in JNR (a), whereas in WMR (b) there were no differences among habitat types. Upper black lines indicate significant differences between habitat types (** = $p < 0.01$). Boxplots represent the median (thicker black horizontal line), inter-quartile range and maximum and minimum values (whiskers).

The structure of fynbos sites was primarily made up by a combination of shrubs, native leaf litter and grass, whereas pine forest sites mainly comprised of pine leaf litter, tree trunks and pine trees in both JNR and WMR (Figures 2.4.9a and b). For WMR, invaded sites differed from one another, with grass, shrubs and native leaf litter making up most of the % cover in semi-invaded fynbos sites while heavily-invaded fynbos mainly comprised of bare ground, grass and native leaf litter (Figure 2.4.9b). Eigenvalues of the first and second PCA axes explained 94.2 % of the cumulative variance for JNR, with the first PCA explaining most of this variation (90.3 %). The distance biplot (Figure 2.4.10a) shows distinct clusters between sites in fynbos from those in pine, indicating that habitat structure differed substantially between these two habitat types. The correlation biplot (Figure 2.4.10b) clearly illustrates the weight of the first PC axis with pine related variables (pine trees, pine tree leaf litter, invasive trees and tree trunks) being in the opposite plane to those associated with fynbos (native trees and leaf litter, shrubs and termite mounds, and see Table 2.4.5). Also, most variables pertaining to pine were highly correlated (Figure 2.4.10b). In WMR, the first two PCA axes explained 84.8 % with the first axis explaining 75.7 % of the variation. The first axis is clearly

illustrated in Table 2.4.5 and the correlation biplot in Figure 2.4.10d where vectors such as pine trees, pine tree leaf litter and tree trunks contrast to those of native trees, shrubs, grass and native leaf litter. In this location, invasive trees are highly correlated with logs and grass is highly correlated with native leaf litter. The distance biplot (Figure 2.4.10c) also illustrates the clustering of sites belonging to each habitat type, indicating that habitat structure variables changed among these clusters.

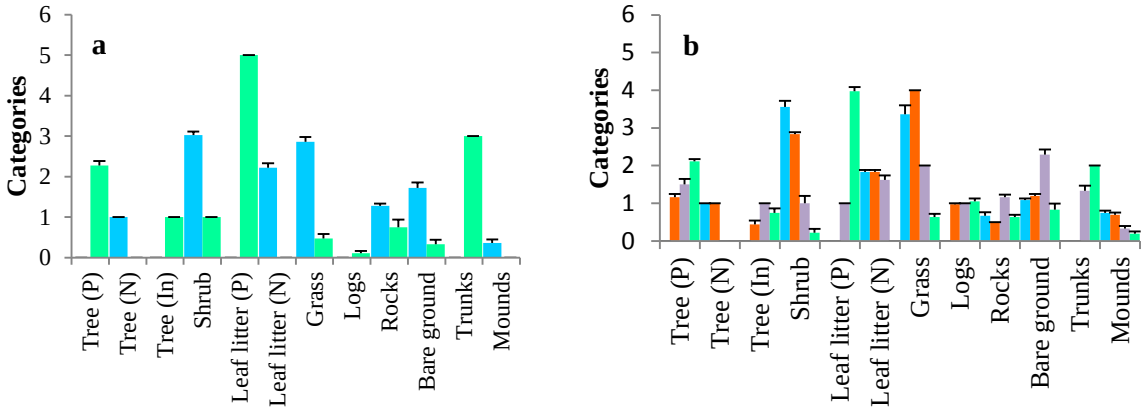


Figure 2.4.9. Percentage cover (mean + SE) presented as categories of environmental variables recorded in JNR (a) and WMR (b) of fynbos (blue), semi-invaded fynbos (orange), heavily-invaded fynbos (purple) and pine forest (green) habitats over four sampling periods (summer 2012, autumn 2013, spring 2013 and autumn 2014). Categories: 1:0-5 %; 2: 6-25 %; 3: 26-50 %; 4: 51-75 %; 5: 76-95 %; 6: 96-100 %. P: pine; N: native; In: invasive (other than *P. radiata*).

Table 2.4.5. Principal component analysis scores of habitat structure variables recorded for the first two axes for JNR and WMR.

| | JNR | | WMR | |
|---|---|---|---|---|
| | PC1 | PC2 | PC1 | PC2 |
| Pine tree | 0.720 | 0.020 | 0.558 | -0.332 |
| Native tree | -0.420 | -0.009 | -0.485 | 0.074 |
| Invasive tree | 0.420 | 0.009 | 0.303 | -0.298 |
| Shrub | -0.412 | -0.012 | -0.879 | 0.045 |
| Leaf litter (pine) | 1.091 | 0.023 | 1.026 | 0.153 |
| Leaf litter (native) | -0.707 | -0.003 | -0.633 | -0.235 |
| Grass | -0.620 | -0.131 | -0.673 | -0.217 |
| Logs | 0.057 | 0.016 | 0.300 | -0.308 |
| Rocks | -0.223 | -0.382 | 0.066 | -0.082 |
| Bare ground | -0.474 | -0.125 | -0.100 | -0.234 |
| Tree trunks | 0.839 | 0.017 | 0.753 | -0.026 |
| Mounds | -0.172 | -0.023 | -0.270 | 0.025 |

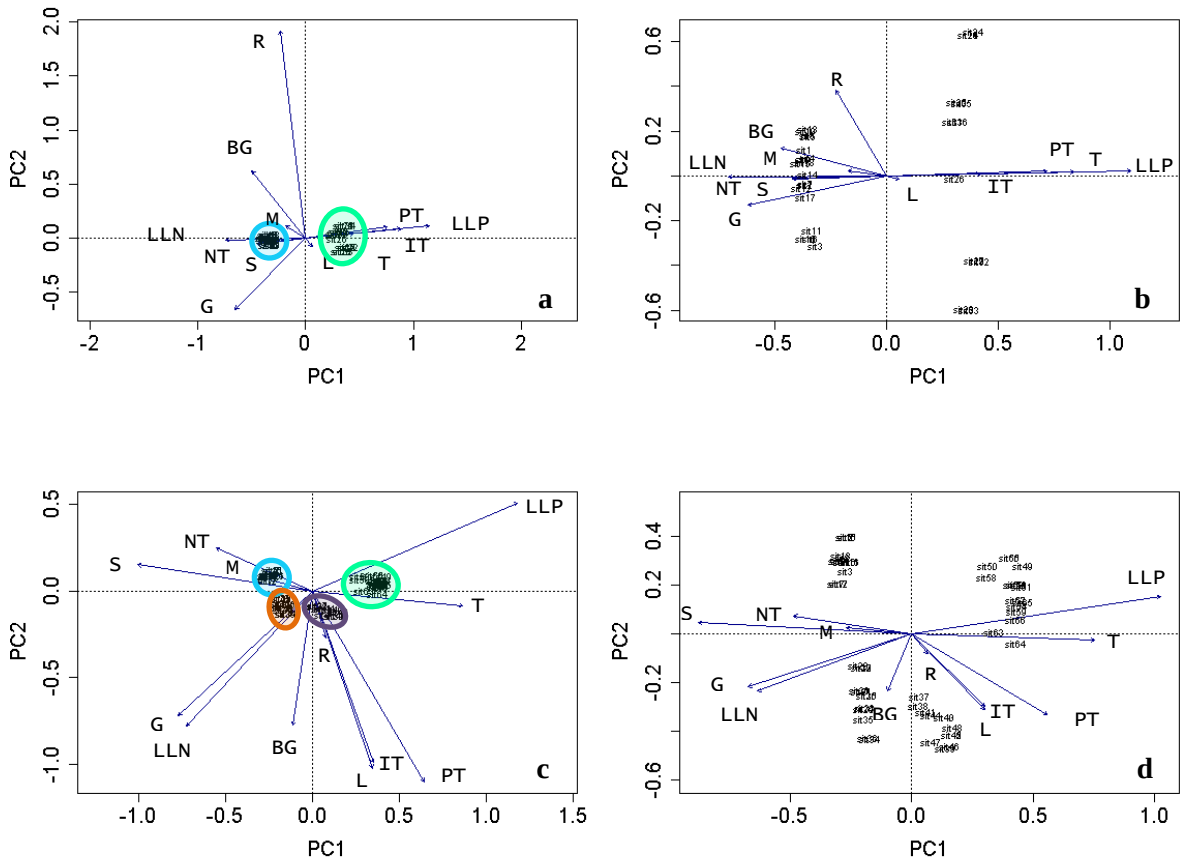


Figure 2.4.10. Principal component analysis (PCA) distance biplot (scaling one) incorporating all habitat structure variables for JNR (a) and WMR (c) and PCA correlation biplot (scaling two) for JNR (b) and WMR (d). Habitat structure variables were: G: grass; R: rocks; S: shrubs; L: logs; M: termite mounds; BG: bare ground; T: tree trunks; PT: pine tree; IT: invasive tree (other than *P. radiata*); NT: native tree; LLP: leaf litter (pine); LLN: leaf litter (native). In (a) and (c) fynbos sites are shaded in blue, semi-invaded fynbos in orange, heavily-invaded fynbos in purple and pine forest in green. In JNR, sit1-18 are fynbos sites and sit19-36 are pine forest sites. In WMR, sit1-18 are fynbos sites, sit18-36 are semi-invaded sites, sit37-48 are heavily-invaded sites and sit49-66 are pine forest sites.

Resources sampling reflected high diversity of taxonomic groups, with Acari, Collembola and Hymenoptera dominating in all habitat types in both JNR (Figure 2.4.11) and WMR (Figure 2.4.12). In JNR, mean abundance of all arthropods sampled during 4 sampling periods (summer 2012, autumn 2013, spring 2013 and autumn 2014) was highest in fynbos (143.2 ± 17.8) than pine forest (54.7 ± 16.3). In WMR, mean abundance was highest in semi-invaded fynbos (109.5 ± 23.9), followed by fynbos (78.3 ± 12.8), heavily-invaded fynbos (65.5 ± 9.3) and pine forest (46.0 ± 8.9). Arthropod community structure differed between pine and fynbos

in JNR (global R = 0.354, P = 0.001, number of permutations = 999; Figure 2.4.13a) and among habitat types in WMR (global R = 0.099, P = 0.001, number of permutations = 999; Figure 2.4.13c). In WMR, the community structure in all habitat types was significantly different from that in the pine forest (Table 2.4.6). Furthermore, analyses using presence-absence data found similar results with distinct arthropod assemblages between fynbos and pine in JNR (global R = 0.117, P = 0.002, number of permutations = 999; Figure 2.4.13b) and among habitat types in WMR (global R = 0.091, P = 0.003, number of permutations = 999; Figure 2.4.13d).In WMR, the only distinction was that the presence-absence data analysis indicated that community composition in heavily invaded fynbos did not differ from that of the pine forest (Table 2.4.6).

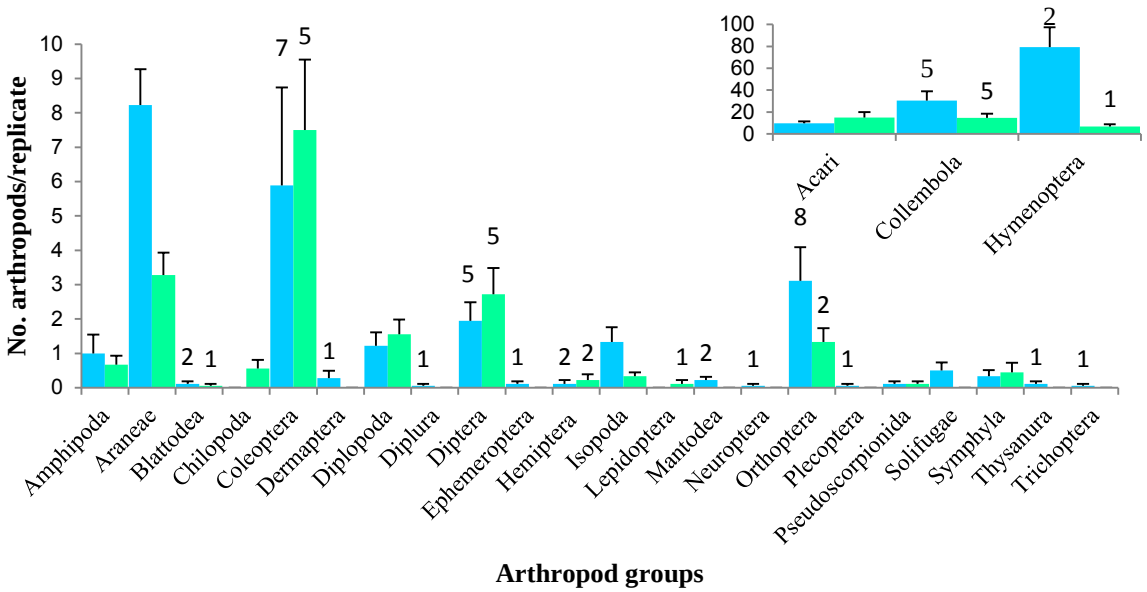


Figure 2.4.11. Abundance data (mean number of individuals per replicate + SE) for each arthropod group collected from pitfall traps, Berlese-Tullgren litter extractions and bush beating samples in fynbos (blue) and pine forest (green) over four sampling periods (summer 2012, autumn 2013, spring 2013 and autumn 2014) in JNR. Numbers at the top of error bars show number of families recorded within an insect order, no number indicates that these arthropods were identified only to order level. Acari, Collembola and Hymenoptera groups had proportionally much higher abundance in both habitat types and are therefore shown in the inset for illustrative purposes.

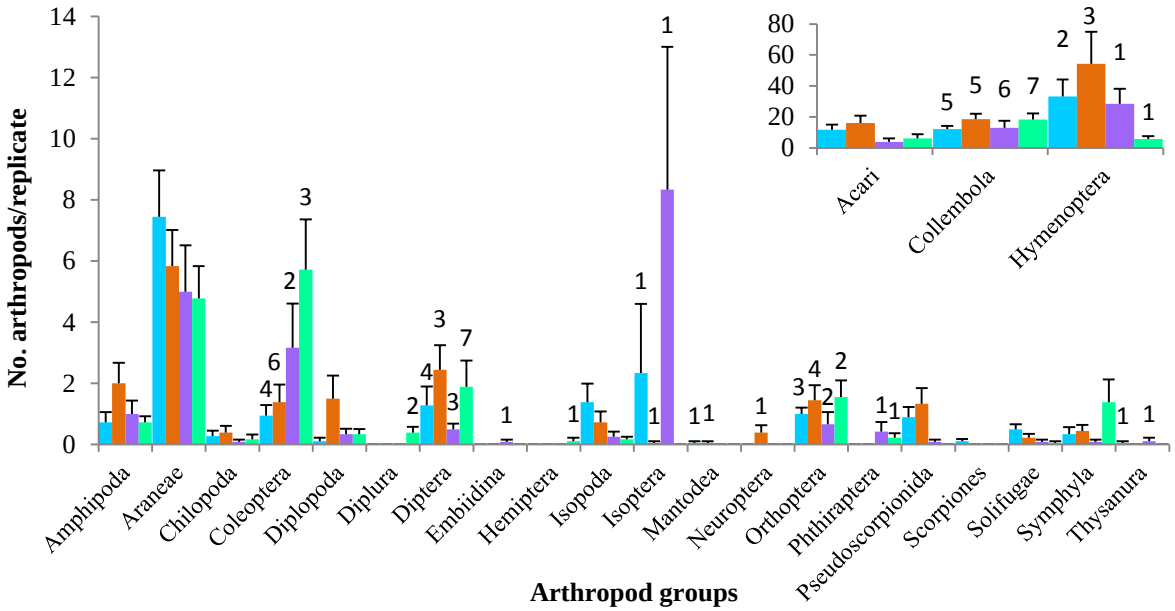


Figure 2.4.12. Abundance data (mean number of individuals per replicate + SE) for each arthropod group collected from pitfall traps, Berlese-Tullgren litter extractions and bush beating samples in fynbos (blue), semi-invaded fynbos (orange), heavily-invaded fynbos (purple) and pine forest (green) over four sampling periods (summer 2012, autumn 2013, spring 2013 and autumn 2014) in WMR. Numbers at the top of error bars show number of families recorded within an insect order, no number indicates that these arthropods were identified only to order level. Acari, Collembola and Hymenoptera groups had proportionally much higher abundance in both habitat types and are therefore shown in the inset for illustrative purposes.

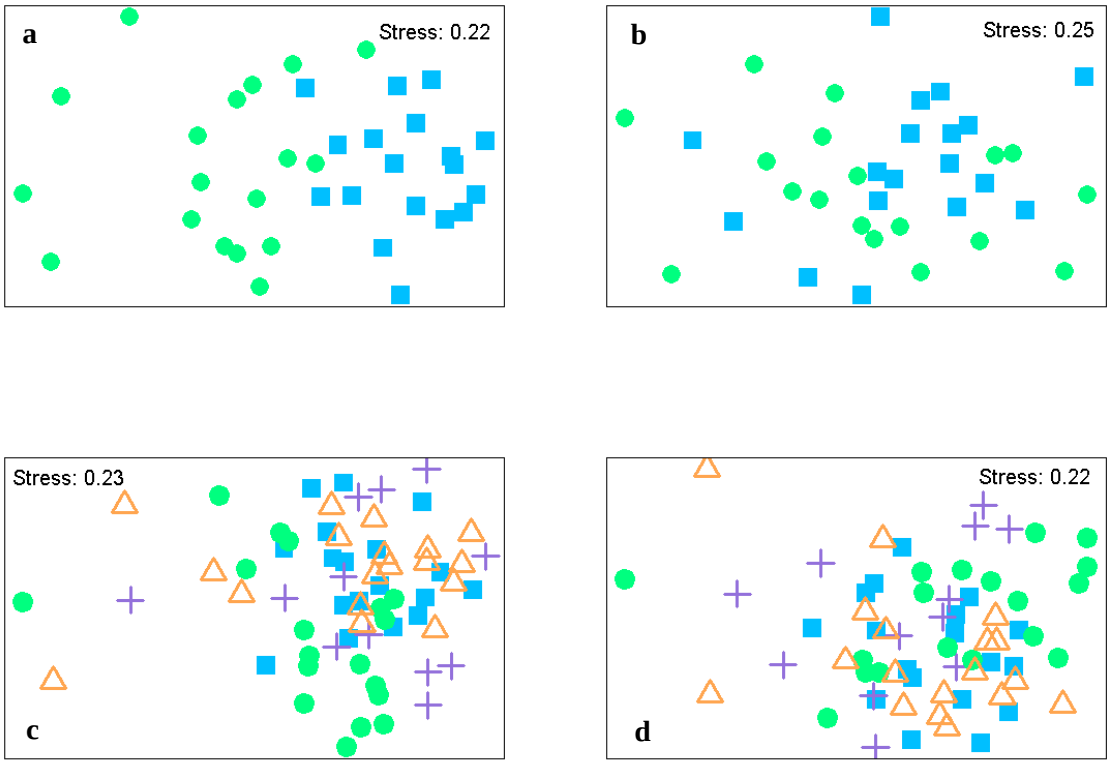


Figure 2.4.13. NMDS ordination of Bray-Curtis similarities based on square-root-transformed arthropod abundance data in JNR (a) in WMR (c), and presence/absence data in JNR (b) and WMR (d). Blue squares are samples from fynbos, orange triangles are samples from semi-invaded fynbos, purple crosses are samples from heavily-invaded fynbos and green circles are samples from pine forest. Symbols represent samples taken from each site within a habitat type over four sampling periods (summer 2012, autumn 2013, spring 2013 and autumn 2014).

Table 2.4.6. Analysis of similarity (ANOSIM) results comparing arthropod assemblages among habitat types in WMR based on Bray-Curtis similarity of square-root transformed abundance data (global R = 0.099, P = 0.001) and presence-absence data (global R = 0.091, P = 0.003).

| | Abundance | | Presence-Absence | |
|---|---|---|---|---|
| Habitat | R statistic | *P* | R statistic | *P* |
| Fyn~Semi | -0.001 | 0.50 | 0 | 0.45 |
| **Fyn~Heavily** | 0.105 | 0.052 | **0.132** | **< 0.05** |
| **Fyn~Pine** | **0.193** | **< 0.001** | **0.176** | **< 0.001** |
| Semi~Heavily | 0.063 | 0.15 | 0.068 | 0.11 |
| **Semi~Pine** | **0.128** | **< 0.01** | **0.102** | **< 0.05** |
| **Heavily~Pine** | **0.103** | **< 0.05** | 0.064 | 0.13 |

### 2.4.3. Relating explanatory variables to lizard abundance

JNR explanatory variables that were retained following the RDA step selection were min $T_e$, max $T_e$, time, pine tree and prey. The amount of explained variance of the species abundance matrix by the explanatory variables was 96 % (adjusted $R^2$ = 0.86, Borcard *et al*. 2011, p.160, Numerical Ecology with R) with 93.4 % explained by the first two canonical axes, the first axis alone explaining 61 % (see Appendix E for RDA model results). The most significant explanatory variables were max $T_e$, min Te, time and pine tree (Table 2.4.7) and this is reflected in the scaling 1 distance triplot (Figure 2.4.14a). From the scaling 2 correlation triplot, *T. homalocephala* is correlated with max $T_e$ and pine tree while *A. atra*, *C. cordylus* are correlated with another set of explanatory variables: time and prey (Figure 2.4.14b). Two species (*T. seps* and *T. capensis*) are grouped together at the centre of the plot indicating that they do not correlate with any particular explanatory variable or that they are related to intermediate environmental conditions. The former is likely as both species were very low in abundance (Table 2.4.1) When variables were grouped into categories (1. habitat structure: pine tree; 2. thermal landscape: min $T_e$, max $T_e$, time; 3. prey) to determine the partitioning of the variance of lizard abundance in JNR, the thermal category and the joint effect of all sets explained most of the variation, 33 % and 25 %, respectively (Figure 2.4.15a).

WMR explanatory variables that were retained following the step selections were min $T_e$, max $T_e$, pine tree, leaf litter (native) and relative humidity. The amount of explained variance of the species abundance matrix by the explanatory variables was 54.6 % (adjusted $R^2$ = 0.32) with 49.4 % explained by the first two canonical axes, the first axis alone explaining 31.4 %

(see Appendix E for RDA model results). The most significant explanatory variables were leaf litter (native) and relative humidity (Table 2.4.7, Figure 2.4.14c). The first axis contrasts *T. homalocephala* and *T. seps* which are mainly correlated with max $T_e$, leaf litter (native), RH %, with the second plane which contains pine tree and *T. capensis* (Figure 2.4.14d). The 5 species grouped centrally likely indicate that they were not particularly related to any particular environmental conditions. Variables were grouped into three categories (1. habitat structure: pine tree and leaf litter (native); 2. thermal landscape: min $T_e$ and max $T_e$; 3. relative humidity) to determine the partitioning of the variable of lizard abundance in WMR. The spatial category and relative humidity explained most of the variation, 27 % and 18 %, respectively (Figure 2.4.15b).

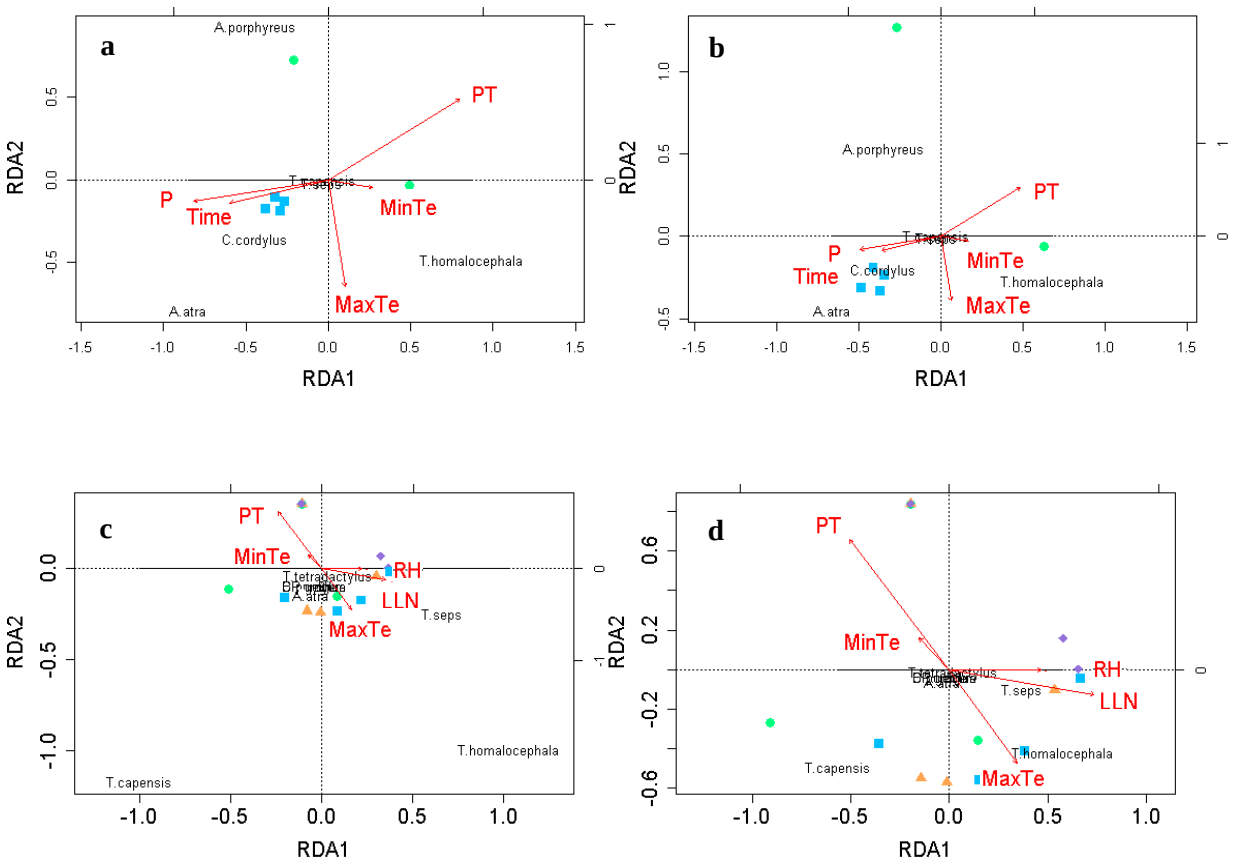


Figure 2.4.14. RDA distance triplots of JNR (a) and WMR (c), scaling one. RDA correlation triplots of JNR (b) and WMR (d), scaling two of fynbos (blue), semi-invaded fynbos (orange), heavily-invaded fynbos (purple) and pine forest (green) habitats over four sampling periods (summer 2012, autumn 2013, spring 2013 and autumn 2014. Lizard species are in black and environmental variables are in red (PT: pine tree; P: arthropod abundance; Min $T_e$: daily minimum $T_e$; Max $T_e$; daily maximum $T_e$; Time: number of hours $T_{sel}$ range was available; LLN: leaf litter (native); RH: relative humidity (%)). A total of four samples per habitat type; due to similarity some are overlaid on top of one another.

Table 2.4.7. *F*-statistic and *p*-values of variables selected for RDA analyses in JNR and WMR.

| Variable | *F*-statistic | *p*-value |
|---|---|---|
| *JNR* | | |
| **Max $T_e$** | **8.236** | **< 0.05** |
| **Min $T_e$** | **9.542** | **< 0.05** |
| **Time** | **20.577** | **< 0.05** |
| **Pine tree** | **8.545** | **< 0.05** |
| Prey | 0.678 | 0.548 |
| *WMR* | | |
| Max $T_e$ | 1.543 | 0.200 |
| Min $T_e$ | 1.592 | 0.218 |
| Pine tree | 1.349 | 0.268 |
| **Leaf litter (native)** | **3.584** | **< 0.05** |
| **Relative humidity** | **3.967** | **< 0.01** |

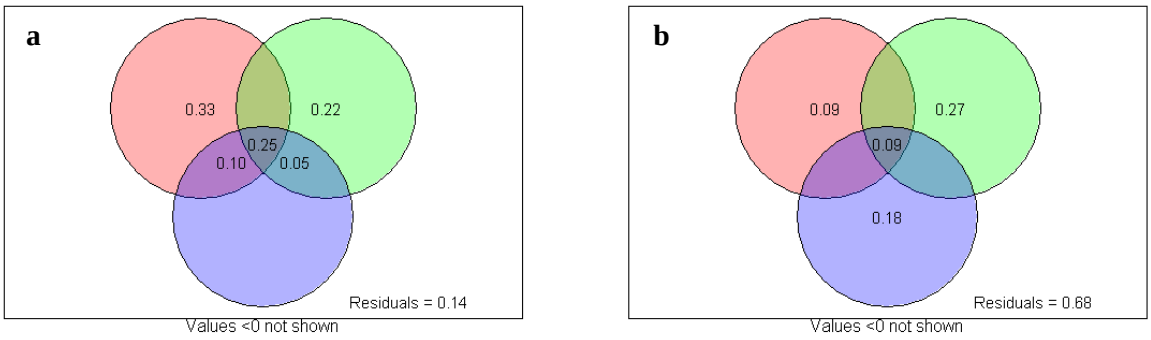


Figure 2.4.15. Venn diagram of the partitioning of the response data (lizard abundance) explained by certain groups of environmental variables. In JNR (a) red: thermal landscape variables (Min $T_e$: daily minimum $T_e$; Max $T_e$: daily maximum $T_e$; Time: number of hours $T_{sel}$ range was available); green: habitat structure variables (pine tree); blue: prey. In WMR (a) red: thermal landscape variables (Min $T_e$: daily minimum $T_e$; Max $T_e$; daily maximum $T_e$; green: habitat structure variables (pine tree; leaf litter (native); purple: relative humidity. The adjusted $R^2$ values are given.

## 2.5 Discussion

At both field locations, lizard species richness, abundance and diversity were positively associated with habitat complexity, with pine forest being lower than native fynbos. In WMR, along the invasion gradient, lizard richness, abundance and diversity in semi-invaded fynbos was higher than heavily-invaded fynbos. These results meet my predictions of lizard species richness and abundance being positively associated with habitat complexity, where fynbos is more complex than pine, and that along the invasion gradient, intermediate values were found for lizard richness and abundance (Figures 2.1a and b). In addition, lizard richness and abundance in semi-invaded fynbos did not differ significantly from fynbos, suggesting these habitat types are similar, but these variables were lower in the heavily-invaded fynbos and pine forest sites (Figure 2.4.1). Interestingly, heavily-invaded fynbos had the lowest diversity of all habitat types, including pine (Figure 2.4.3); as opposed to prior expectations that the increased complexity in this habitat originating from the mixture of native and alien vegetation may increase species richness and abundance. For example, Bateman and Ostoja (2012) found that lizard species were more abundant in mixed (native and alien) habitat types than pure alien habitats, where certain species were associated with specific structural habitat features, i.e. native trees, open habitats with low canopy or shrub cover for greater basking opportunities or openness required for locomotion (Rieder *et al*. 2010). In South Africa, reptile and amphibian assemblages differ between natural vegetation types and plantation and cultivated habitats, with natural sites harbouring the highest richness and abundance (Trimble & van Aarde 2014).

In this study, low species dominance was present in pine forest and heavily-invaded fynbos, which indicates that the few species encountered in these habitats were evenly distributed. Furthermore, lizard community structure clearly differed between fynbos and pine forest sites in JNR and WMR (Figure 2.4.5). Additionally, in WMR, fynbos and heavily-invaded fynbos were also different. Lizards avoiding alien plant habitats have previously been shown where IAPs altered the native vegetation structure in such a way that was thought to be unfavourable to reptiles, and ultimately negatively affected lizard richness, abundance and diversity (Valentine 2006; Valentine *et al*. 2007; Bateman *et al*. 2008; Bateman & Ostoja 2012; Stellatelli *et al*. 2013; Trimble & van Aarde 2014). Furthermore, in this study, I found clear differences in lizard communities between fynbos habitats from JNR and WMR (see Appendix E), but assemblages in pine forests did not differ between locations, which indicates the homogeneity of pine habitats. Thus, altered microhabitats may drive the low abundance, richness and diversity observed in pine forest and heavily-invaded fynbos.

This study has shown that habitat structure is highly differentiated between fynbos and pine (see figure 2.4.10, clear clustering of sites across habitat types in PCAs) and among the four habitat types along the invasion gradient in WMR. Moreover, pine variables strongly contrast to native variables in both JNR and WMR. Habitat structure can directly affect thermal landscapes (e.g. Valentine *et al*. 2007, Stellatelli *et al*. 2013) and I found that habitat thermal quality differed across habitat types with the poorest quality found in the pine forest in both JNR and WMR. In both locations, during the peak lizard activity period (10h00-12h00 and 15h00-17h00, pers. obs.) operative temperatures recorded within open and closed canopy sites, in fynbos and intermediately invaded sites, fell within the preferred body temperature range of lizard families encountered in this study (Figure 2.4.6.). By contrast, open and closed canopy sites in the pine forest rarely provided operative temperatures which fell within the temperature range targeted by lizard families found within the Western Cape. This was true for both locations. The body temperature of lizards is largely dependent upon habitat temperature (Heatwole & Taylor 1987) and fynbos and intermediately invaded sites provide a more thermally suitable environment. Similarly, Mott *et al*. (2010) found that cooler conditions and lower radiant energy levels were experienced in exotic pine plantations than in native forests of tropical northern Australia. In consequence, pine plantations consisted mainly of reptile assemblages of closed canopy rainforest species, which have a preference for shadier, cooler habitats as compared to the nearby native vegetation which mostly included woodland species.

In JNR and WMR, operative temperatures ($T_e$) experienced in the pine forest were more buffered compared to other habitat types. Taller trees and denser canopy cover of the pine trees likely reduce the amount of sunlight reaching the forest floor where operative models were located (Appendix C). Various studies have shown that vegetation types with a dense canopy result in thermal restrictions and ultimately limiting availability of basking and thermoregulatory opportunities for ectotherms (House & Spelleberg 1983; Sartorius *et al*. 1999). For both locations, in open and closed canopy sites, pine forest sites reached mean $T_{sel}$ at the slowest rate. Furthermore, in both locations, fynbos and intermediately invaded sites had a high frequency of favourable $T_e$s whereas pine forest sites had a substantially lower frequency (Figure 2.4.7) providing lizards with reduced optimal microsites. The availability of thermoregulatory opportunities is essential for several physiological and behavioural features in ectotherms (Huey & Kingsolver 1989; Angilletta *et al*. 2002). In both locations, fynbos and intermediately invaded fynbos sites are thermally more heterogeneous than pine forest, presenting lizards with a wider range of basking opportunities. Survival ability and the

procurement of resources for lizards can be strongly constrained by environmental temperatures and have been shown to restrict lizard ranges (Huey 1982; Kearney & Porter 2004; Buckley & Rougharden 2006; Buckley 2008).

This study showed that arthropod abundance and composition followed a similar trend to lizard assemblages, where the quantity and quality of prey varied across habitat types. Pine forest had the lowest abundance for both JNR and WMR sampling locations. In WMR, pine forest arthropod abundance clearly differed from all other habitats, while pine forest arthropod composition did not differ from heavily-invaded fynbos (Figure 2.4.13). Changes in presence and abundance of certain arthropod species could be attributed to the fact that native arthropods are not able to recognize novel plant species (Tallamy 2004). Presence of IAPs could have varying effects on arthropod assemblages but for many groups it results in a decrease in abundance and/or richness (Litt *et al*. 2014), consequently affecting lizard assemblages which are dependent on arthropods as resources. Even though a broad range of arthropods were collected in all habitat types, the differences in arthropod community structure may provide varied foraging opportunities for lizards, where those in heavily-invaded fynbos and pine forest are inferior in terms of species abundance but likely also in food resource quality for lizards.

Differences in lizard diversity across habitat types are likely associated with a combination of habitat structure, thermal quality, prey abundance and relative humidity but combined analyses point to presence of pine and thermal variables, such as max $T_e$, being important drivers of these lizard assemblages. However, while the study highlights clear differences in lizard species richness, abundance and diversity reflecting the impact of pine plantations and invasions and the effects that these have on the thermal landscape and resources available, the mechanisms driving differences in lizard assemblages is difficult to ascertain. The unexpected low number of captures despite the effort means that a much larger number of replicates and locations would have to be sampled to improve the robustness of the inferences made. However, an experimental approach testing the mechanistic hypotheses directly (e.g. multifactorial design with field cage experiments that incorporate differences in habitat temperature quality and/or resources) may be more cost-effective.

In conclusion, this study presents important findings of the clear negative effects of pine forest and pine invasions on lizard diversity generally found in native fynbos. Overall, pine forests provided suboptimal habitats in comparison to native and intermediately invaded fynbos, by thermally being more homogeneous and supporting less abundant and dissimilar

prey resources. However, further work and possible experimentation is needed to ascertain cause and effect and disentangle the mechanism driving lizard species loss, it being loss of thermal habitat quality, loss of prey abundance and diversity, or both.

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# Chapter 3

## 3.1 Conclusion

This study quantified species richness, abundance and diversity of lizard assemblages in native fynbos, intermediately invaded fynbos and pine forests in the CFR. Heavily-invaded fynbos and pine forests support a lower species richness, abundance and diversity of lizard assemblages in contrast to native and semi-invaded fynbos. The thermal landscape is vastly different in pine forests compared to fynbos and intermediate invaded sites, presenting fewer thermal opportunities which are within the preferred range of temperatures for species of Western Cape lizards. Furthermore, clear differences in the availability of resources across habitat types were shown. Based on these results, I suggest that in areas where *Pinus radiata* are invading native fynbos, lizard assemblages will be disadvantaged by the replacement of native habitat with a thermally and nutritionally sub-optimal environment. The absence and low abundance of lizards in these environments are likely to have a knock-on effect on higher order predators, such as larger reptiles and birds which rely on them as prey. Given these impacts, alongside an understanding of changes in ecological processes (such as plant species composition (Richardson & van Wilgen 2004), fire (D'Antonio & Vitousek 1992; Rossiter *et al*. 2003), nutrient (Vitousek & Walker 1989; Witkowski 1991; Evans *et al.* 2001) and hydrological (Le Maitre *et al*. 1996; Blossey 1999) cycles), *Pinus radiata* represents a substantial threat to reptile biodiversity in the fynbos biome. Of all the lizard species encountered in the study 22 % are endemic to south western region of the Western Cape Province, 56 % to South Africa and 22 % to southern Africa (Alexander & Marais 2007; Branch 1998; Bates *et al*. 2014), with one species (*Bradypodion pumilum*) considered to be vulnerable according to Southern African Reptile Conservation Assessment (De Villiers *et al*. 2010) indicating the significance of conservation of this species and its natural habitat. Currently, JNR is well managed for the spread of *P. radiata* by CapeNature and the Working for Water programme, however, in WMR very little is being done to eradicate or manage invading trees. This study suggests that control of *P. radiata* is vital for the conservation of native lizard assemblages and that a concerted effort is required by both governmental organisations and private landowners to minimize the spread of IAPs in the area. Knowledge of the mechanisms underlying differential use of native and invasive plant habitats by vertebrate ectotherms is crucial for understanding how IAPs alter the environment and will enable managers to better predict faunal responses to disturbances from IAPs.

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# Appendix A. Lizard sampling methods

## Pitfall traps

Pitfall traps were white 10 L plastic buckets sunken into the ground such that the lip of the bucket was flush with the ground level. Each bucket had five small drainage holes (0.4 cm) drilled into the bottom of the bucket. Each Y-array contained four pitfall buckets, one at the centre where the three arms joined and one at the end of each arm. White bucket lids were propped 8 cm above pitfalls using plastic props, to cast shade and protection. In addition, wet cloths and moist leaf litter were placed within each pitfall to create additional protection. The lids were closed between sampling periods to prevent accidental animal captures.

## Funnel traps

Double-ended funnel traps were constructed using 0.2 cm wire mesh. Funnel traps were 75 cm x 15 cm cylinders, with a zip fitted at the top of the funnel. Openings in the inverted funnel cones were 5 cm in diameter. Two funnel traps were placed in juxtaposition alongside each arm of the Y-array. Each funnel trap was covered with a wooden board to provide shade for trapped animals. Zips were left open and the cones were pulled out between sampling periods to avoid accidental animal captures.


Figure A. Lizard Y-array traps in native mountain fynbos (1) and pine forest (2). (Photos: S. Clusella-Trullas).

## Appendix B. Copper model calibrations

To test for variation across multiple copper models, infra-red lights (175 W, General Electric Company, Johannesburg, South Africa) were suspended, *ca.* 30 cm, directly above seven copper models in a temperature controlled room (18 °C). Models started recording after 20 minutes, at five minute intervals, in order to adjust to the temperature within the room. After 80 minutes the temperature was increased by switching on the infra-red lights. Once models had stabilized, mean operative temperature ($T_e$) during the cold period was 18.3 ± 0.1 °C (mean ± SE) and mean $T_e$ during the warm period was 58.1 ± 0.5°C. The standard error for all models at a given time was 0.5 °C in average, illustrating little $T_e$ variation among models.

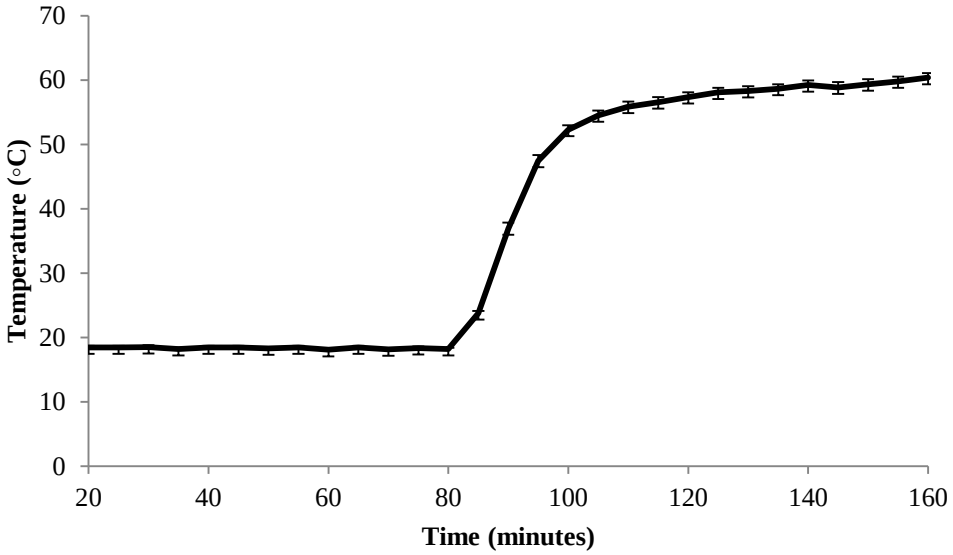


Figure B. Temperature responses (mean ± SE) of 7 lizard models in a temperature controlled room in the laboratory. Models experienced cold temperatures from 20-80 minutes, after 80 minutes temperature was increased and warm temperatures were experienced from 105-160 minutes.

## Appendix C. Descriptive statistics of operative temperatures and pine tree measurements of Jonkershoek Nature Reserve and Witzenberg Mountain Range

Table C.1. Summary of mean, maximum and minimum operative temperatures ($T_e$) for open and closed canopy sites of each habitat type of JNR and WMR. All values are in °C ± SE.

| Location | Canopy | Temperature | F | SI | HI | P |
|---|---|---|---|---|---|---|
| JNR | O | Mean | 29.9°C ± 0.5 | | | 23.2°C ± 0.2 |
| | C | | 23.0°C ± 0.5 | | | 21.5°C ± 0.2 |
| | O | Max | 72.7°C ± 0.6 | | | 70.2°C ± 1.8 |
| | C | | 51.5°C ± 1.9 | | | 55.7°C ± 2.8 |
| | O | Min | 3.4°C ± 0.4 | | | 5.0°C ± 0.2 |
| | C | | 4.4°C ± 0.3 | | | 4.5°C ± 0.3 |
| WMR | O | Mean | 30.4°C ± 0.4 | 30.1°C ± 0.5 | 31.4°C ± 0.4 | 23.9°C ± 0.3 |
| | C | | 26.3°C ± 0.7 | 26.4°C ± 0.5 | 27.2°C ± 0.4 | 23.0°C ± 0.6 |
| | O | Max | 75.2°C ± 0.8 | 73.8°C ± 0.7 | 71.3°C ± 1.5 | 63.5°C ± 1.3 |
| | C | | 66.4°C ± 2.8 | 67.9°C ± 2.9 | 62.7°C ± 1.4 | 63.4°C ± 2.3 |
| | O | Min | 0.0°C ± 0.4 | 0.6°C ± 0.4 | 3.1°C ± 0.3 | 3.0°C ± 0.2 |
| | C | | 1.9°C ± 0.2 | 1.8°C ± 0.3 | 4.0°C ± 0.4 | 4.6°C ± 0.2 |

Canopy: O, open canopy; C, closed canopy

Habitat type: F, fynbos; SI, semi-invaded fynbos; HI, heavily-invaded fynbos; P, pine forest

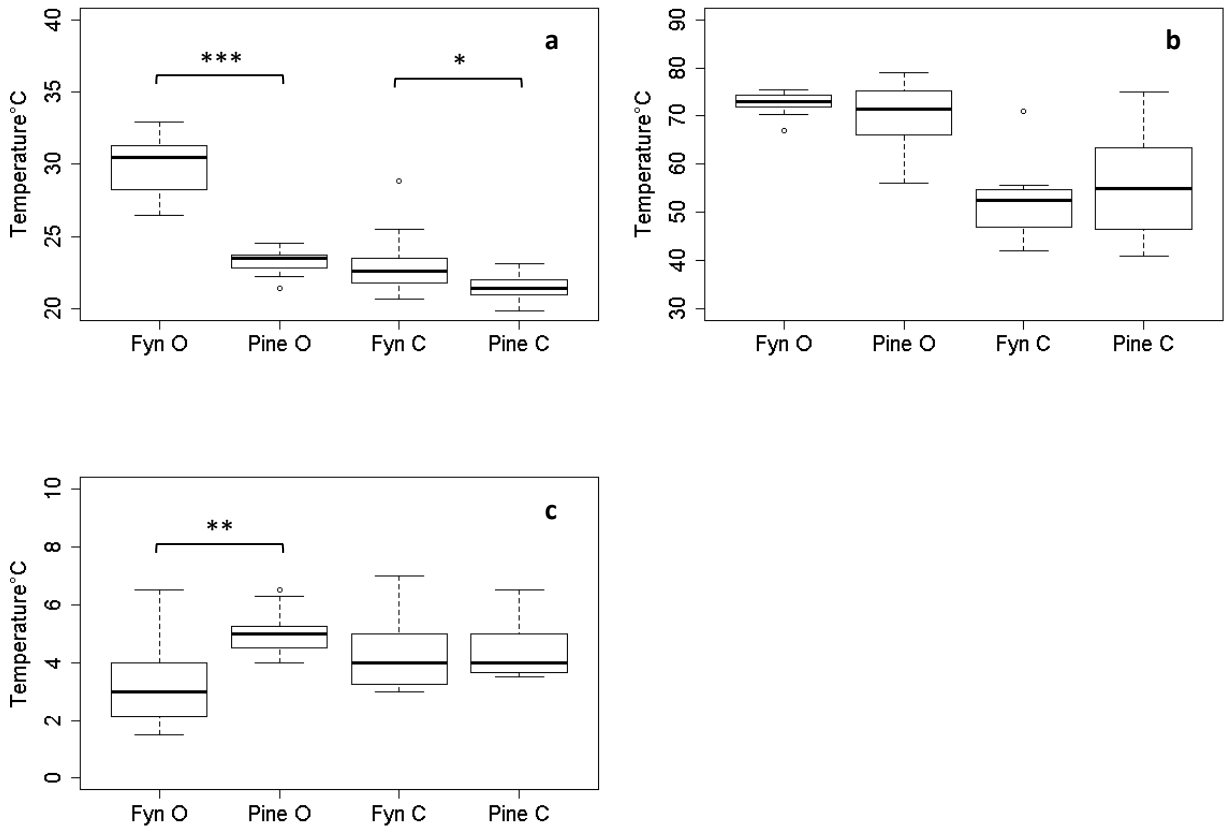


Figure C.1. Mean (a), max (b), min (c) $T_e$ of open and closed canopy sites in JNR. Upper black lines indicate significant differences between habitat types (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$). Boxplots represent the median (thicker black horizontal line), inter-quartile range and maximum and minimum values (whiskers).

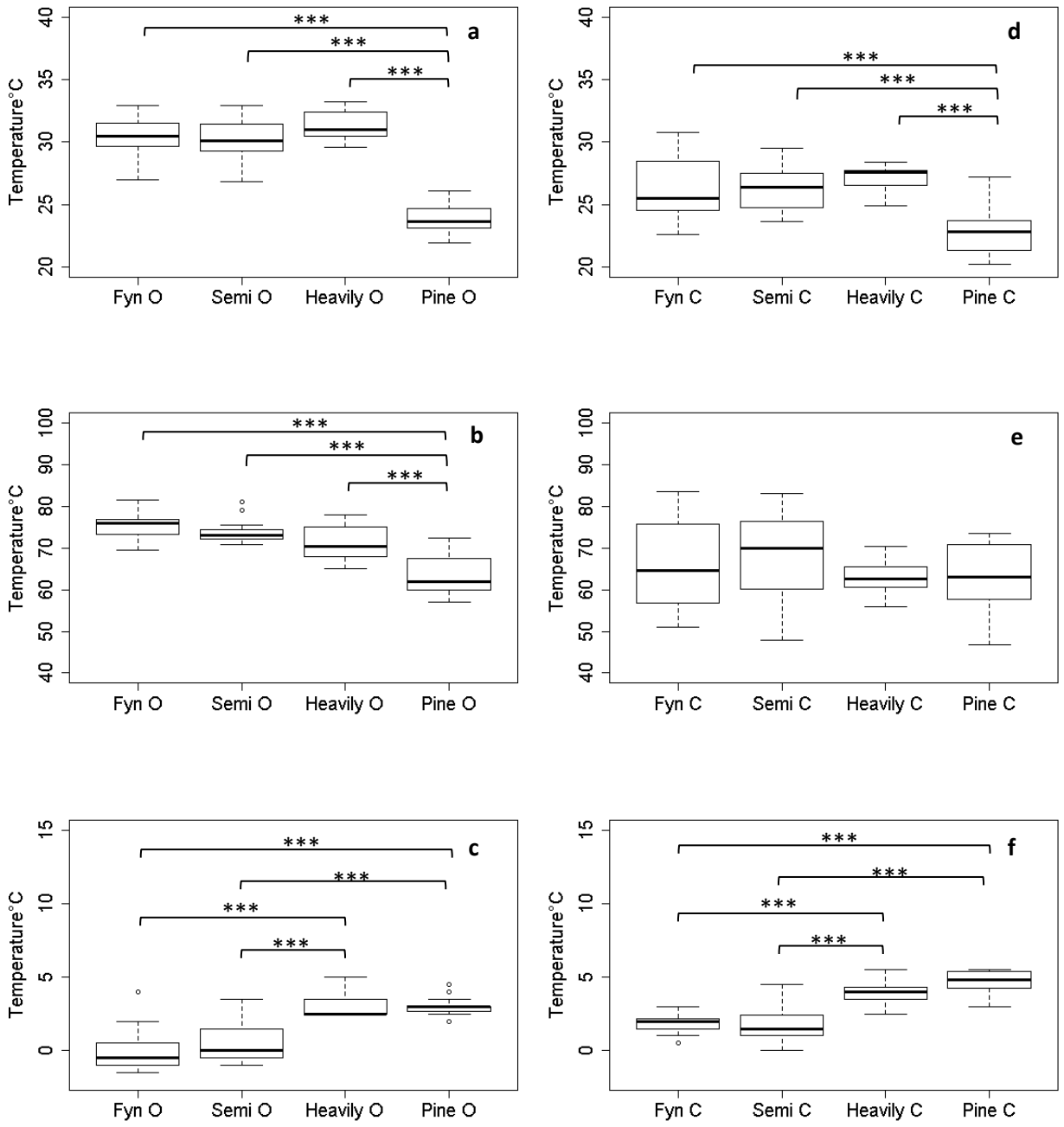


Figure C.2. Mean (a), max (b), min (c) $T_e$ of open canopy sites in WMR and mean (d) max (e) and min (f) of closed canopy sites. Upper black lines indicate significant differences between habitat types (*** = $p < 0.001$). Boxplots represent the median (thicker black horizontal line), inter-quartile range and maximum and minimum values (whiskers).

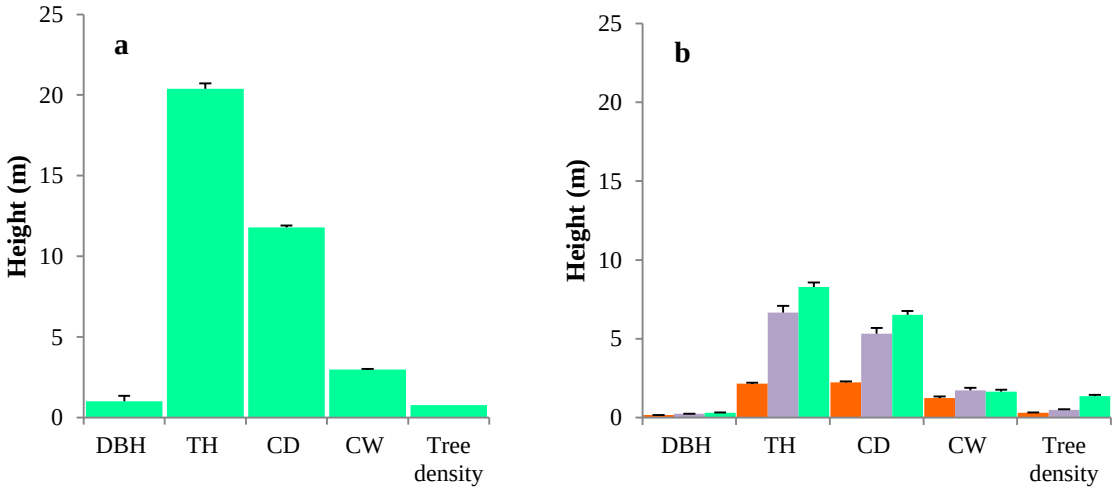


Figure C.3. JNR (a) and WMR (b) pine tree measurements (mean + SE) in semi-invaded fynbos (orange), heavily-invaded fynbos (purple) and pine forest (green) measured over four sampling periods (summer 2012, autumn 2013, spring 2013 and autumn 2014). DBH: diameter breast height taken at 1.3m above ground; TH: tree height; CD: crown depth; CW: crown width; Tree density: number of trees per $m^2$. One 10 $m^2$ plot/site was randomly selected for surveys of standard diameter breast height (DBH at 1.3 m above ground), tree height and crown dimensions which included top-of-crown height, bottom-of-crown height and crown width. Crown depth was calculated by subtracting tree height from the bottom of the crown from the total tree height. The latter was estimated using a handheld laser range finder (Bushnell Laser Rangefinder, Sport450).

**Appendix D. Species accumulation curves for each habitat in Jonkershoek Nature Reserve and Witzenberg Mountain Range**

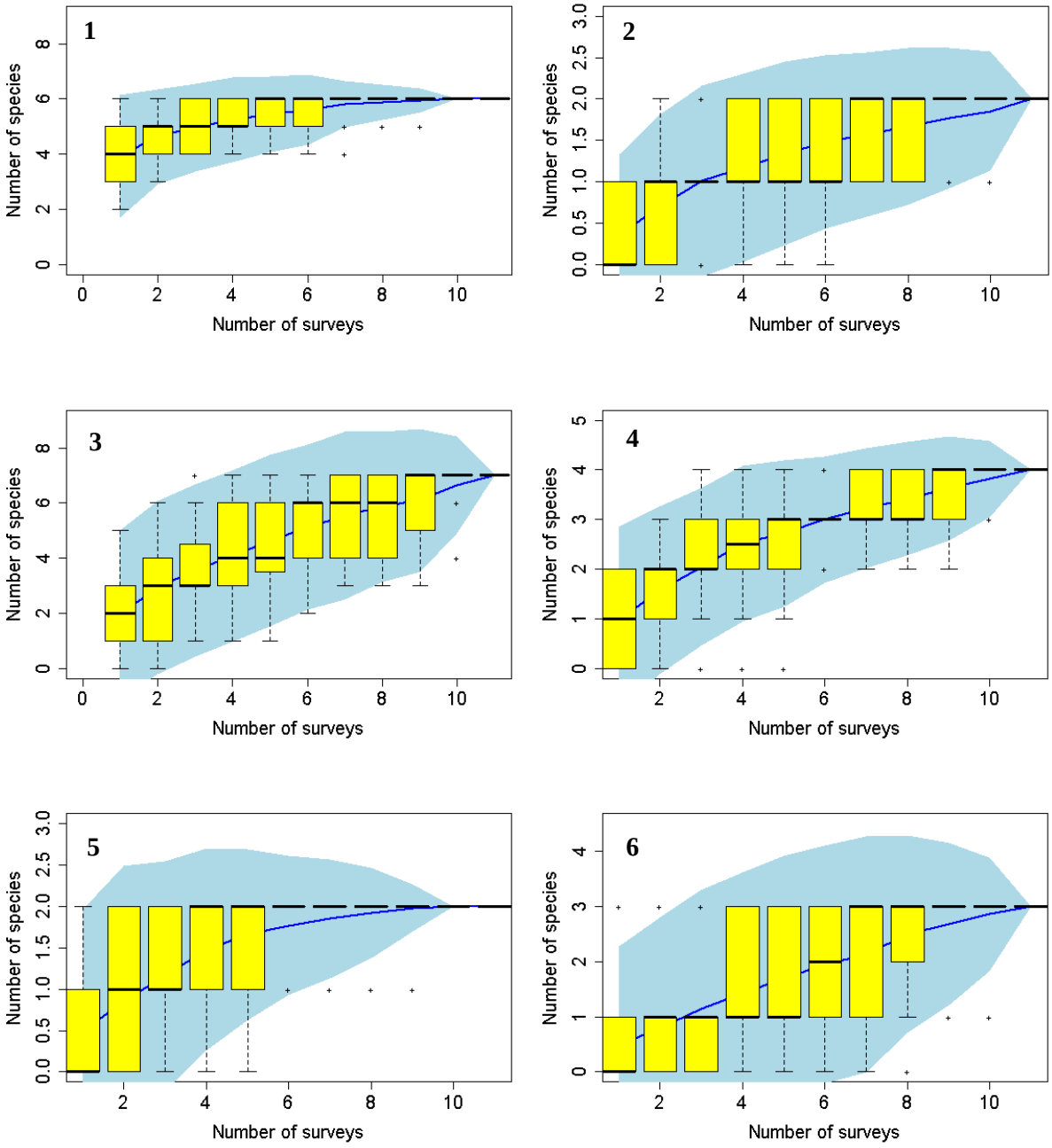


Figure D. Species accumulation curves for JNR fynbos (1) and pine forest (2), and WMR fynbos (3), semi-invaded fynbos (4), heavily-invaded fynbos (5) and pine forest (6). Boxplots represent the median (thicker black horizontal line), inter-quartile range and maximum and minimum values (whiskers).

## Appendix E. Correlation matrices of environmental variables

Table E.1. JNR correlation matrix of environmental variables considered for RDA. The variables in bold were those selected for the RDA analyses. PT: pine tree; NT: native tree; IT: invasive tree (other than *P. radiata*); S: shrub; LLP: leaf litter (pine); LLN: leaf litter (native); G: grass; L: logs; R: rocks; BG: bare ground; T: trunks; Prey: arthropod abundance; RH: relative humidity (%); Min $T_e$: daily minimum $T_e$; Max $T_e$; daily maximum $T_e$; Time: number of hours $T_{sel}$ range was available.

| | PT | NT | IT | S | LLP | LLN | G | L | R |
|---|---|---|---|---|---|---|---|---|---|
| **PT** | 1.0000000 | -0.9932659 | 0.9932659 | -0.9932659 | 0.9932659 | -0.9851131 | -0.9776054 | 0.48268187 | -0.93752364 |
| NT | -0.9932659 | 1.0000000 | -1.0000000 | 1.0000000 | -1.0000000 | 0.9917919 | 0.9897783 | -0.37796447 | 0.94387981 |
| IT | 0.9932659 | -1.0000000 | 1.0000000 | -1.0000000 | 1.0000000 | -0.9917919 | -0.9897783 | 0.37796447 | -0.94387981 |
| S | -0.9932659 | 1.0000000 | -1.0000000 | 1.0000000 | -1.0000000 | 0.9917919 | 0.9897783 | -0.37796447 | 0.94387981 |
| LLP | 0.9932659 | -1.0000000 | 1.0000000 | -1.0000000 | 1.0000000 | -0.9917919 | -0.9897783 | 0.37796447 | -0.94387981 |
| LLN | -0.9851131 | 0.9917919 | -0.9917919 | 0.9917919 | -0.9917919 | 1.0000000 | 0.9816541 | -0.37486211 | 0.97836391 |
| G | -0.9776054 | 0.9897783 | -0.9897783 | 0.9897783 | -0.9897783 | 0.9816541 | 1.0000000 | -0.33008914 | 0.93423172 |
| L | 0.4826819 | -0.3779645 | 0.3779645 | -0.3779645 | 0.3779645 | -0.3748621 | -0.3300891 | 1.00000000 | -0.35675303 |
| R | -0.9375236 | 0.9438798 | -0.9438798 | 0.9438798 | -0.9438798 | 0.9783639 | 0.9342317 | -0.35675303 | 1.00000000 |
| BG | -0.9576165 | 0.9702693 | -0.9702693 | 0.9702693 | -0.9702693 | 0.9758113 | 0.9829480 | -0.31783036 | 0.95070593 |
| T | 0.9932659 | -1.0000000 | 1.0000000 | -1.0000000 | 1.0000000 | -0.9917919 | -0.9897783 | 0.37796447 | -0.94387981 |
| M | -0.7693805 | 0.7745967 | -0.7745967 | 0.7745967 | -0.7745967 | 0.7412830 | 0.7666789 | -0.29277002 | 0.66149509 |
| **Prey** | -0.8056924 | 0.7909494 | -0.7909494 | 0.7909494 | -0.7909494 | 0.7908755 | 0.7853896 | -0.45932628 | 0.76314069 |
| **RH** | 0.3480779 | -0.3761036 | 0.3761036 | -0.3761036 | 0.3761036 | -0.3680698 | -0.3739834 | -0.06156267 | -0.34221831 |
| **MinTe** | 0.2997527 | -0.2675656 | 0.2675656 | -0.2675656 | 0.2675656 | -0.3308139 | -0.3280339 | 0.37273742 | -0.42160356 |
| **MaxTe** | -0.2168433 | 0.2419226 | -0.2419226 | 0.2419226 | -0.2419226 | 0.1763279 | 0.1632849 | 0.09595360 | 0.06403349 |
| **Time** | -0.5868571 | 0.5726563 | -0.5726563 | 0.5726563 | -0.5726563 | 0.5148138 | 0.5297568 | -0.36073955 | 0.40324411 |

| | BG | T | M | Prey | RH | MinTe | MaxTe | Time |
|---|---|---|---|---|---|---|---|---|
| **PT** | -0.95761651 | 0.9932659 | -0.7693805 | -0.8056924 | 0.34807786 | 0.29975268 | -0.21684330 | -0.5868571 |
| NT | 0.97026934 | -1.0000000 | 0.7745967 | 0.7909494 | -0.37610360 | -0.26756564 | 0.24192258 | 0.5726563 |
| IT | -0.97026934 | 1.0000000 | -0.7745967 | -0.7909494 | 0.37610360 | 0.26756564 | -0.24192258 | -0.5726563 |
| S | 0.97026934 | -1.0000000 | 0.7745967 | 0.7909494 | -0.37610360 | -0.26756564 | 0.24192258 | 0.5726563 |
| LLP | -0.97026934 | 1.0000000 | -0.7745967 | -0.7909494 | 0.37610360 | 0.26756564 | -0.24192258 | -0.5726563 |
| LLN | 0.97581134 | -0.9917919 | 0.7412830 | 0.7908755 | -0.36806975 | -0.33081394 | 0.17632787 | 0.5148138 |
| G | 0.98294801 | -0.9897783 | 0.7666789 | 0.7853896 | -0.37398339 | -0.32803394 | 0.16328488 | 0.5297568 |
| L | -0.31783036 | 0.3779645 | -0.2927700 | -0.4593263 | -0.06156267 | 0.37273742 | 0.09595360 | -0.3607396 |
| R | 0.95070593 | -0.9438798 | 0.6614951 | 0.7631407 | -0.34221831 | -0.42160356 | 0.06403349 | 0.4032441 |
| BG | 1.00000000 | -0.9702693 | 0.6847614 | 0.7136109 | -0.30094075 | -0.44850846 | 0.03728634 | 0.4156942 |
| T | -0.97026934 | 1.0000000 | -0.7745967 | -0.7909494 | 0.37610360 | 0.26756564 | -0.24192258 | -0.5726563 |
| M | 0.68476141 | -0.7745967 | 1.0000000 | 0.8138874 | -0.71341097 | -0.02566020 | 0.44650293 | 0.8378689 |
| **Prey** | 0.71361090 | -0.7909494 | 0.8138874 | 1.0000000 | -0.31356819 | -0.08893180 | 0.15583081 | 0.7989147 |
| **RH** | -0.30094075 | 0.3761036 | -0.7134110 | -0.3135682 | 1.00000000 | -0.01070846 | -0.55812489 | -0.3634859 |
| **MinTe** | -0.44850846 | 0.2675656 | -0.0256602 | -0.0889318 | -0.01070846 | 1.00000000 | 0.71847064 | 0.3458465 |
| **MaxTe** | 0.03728634 | -0.2419226 | 0.4465029 | 0.1558308 | -0.55812489 | 0.71847064 | 1.00000000 | 0.5205170 |
| **Time** | 0.41569418 | -0.5726563 | 0.8378689 | 0.7989147 | -0.36348586 | 0.34584653 | 0.52051702 | 1.0000000 |

Table E.2. WMR correlation matrix of environmental variables considered for RDA. The variables in bold were those selected for the RDA analyses. PT: pine tree; NT: native tree; IT: invasive tree (other than *P. radiata*); S: shrub; LLP: leaf litter (pine); LLN: leaf litter (native); G: grass; L: logs; R: rocks; BG: bare ground; T: trunks; Prey: arthropod abundance; RH: relative humidity (%); Min $T_e$: daily minimum $T_e$; Max $T_e$; daily maximum $T_e$; Time: number of hours $T_{sel}$ range was available.

| | PT | NT | IT | S | LLP | LLN | G | L | R |
|---|---|---|---|---|---|---|---|---|---|
| **PT** | 1.00000000 | -0.7762155 | 0.88073477 | -0.83813416 | 0.73704213 | -0.6361828 | -5.877815e-01 | 0.93364211 | 3.361112e-01 |
| NT | -0.77621547 | 1.0000000 | -0.85769003 | 0.94934231 | -0.86035025 | 0.6875635 | 8.017837e-01 | -0.57735027 | -5.773503e-01 |
| IT | 0.88073477 | -0.8576900 | 1.00000000 | -0.80598899 | 0.61867775 | -0.4262623 | -4.871080e-01 | 0.80467980 | 6.808829e-01 |
| S | -0.83813416 | 0.9493423 | -0.80598899 | 1.00000000 | -0.92660239 | 0.8276134 | 8.640276e-01 | -0.63698461 | -3.703399e-01 |
| LLP | 0.73704213 | -0.8603503 | 0.61867775 | -0.92660239 | 1.00000000 | -0.9541257 | -9.758356e-01 | 0.49672345 | 8.480644e-02 |
| **LLN** | -0.63618277 | 0.6875635 | -0.42626235 | 0.82761340 | -0.95412572 | 1.0000000 | 9.587430e-01 | -0.39696495 | 1.898528e-01 |
| G | -0.58778155 | 0.8017837 | -0.48710802 | 0.86402765 | -0.97583561 | 0.9587430 | 1.000000e+00 | -0.30860670 | 4.283040e-17 |
| L | 0.93364211 | -0.5773503 | 0.80467980 | -0.63698461 | 0.49672345 | -0.3969650 | -3.086067e-01 | 1.00000000 | 3.333333e-01 |
| **R** | 0.33611116 | -0.5773503 | 0.68088291 | -0.37033989 | 0.08480644 | 0.1898528 | 4.283040e-17 | 0.33333333 | 1.000000e+00 |
| BG | 0.10455931 | -0.2993422 | 0.50706702 | -0.08141321 | -0.21733788 | 0.4635351 | 2.880092e-01 | 0.17282528 | 9.332565e-01 |
| T | 0.78810663 | -0.9878783 | 0.81198951 | -0.97163055 | 0.92823392 | -0.7907932 | -8.800720e-01 | 0.57035183 | 4.436070e-01 |
| M | -0.80844769 | 0.9600769 | -0.77986494 | 0.97890647 | -0.95777071 | 0.8447284 | 9.061604e-01 | -0.59425023 | -3.445653e-01 |
| **Prey** | -0.20190912 | 0.5037776 | -0.17371944 | 0.43735233 | -0.53421695 | 0.4616841 | 5.623106e-01 | -0.05283092 | -1.420904e-01 |
| **RH** | 0.09600082 | -0.2141666 | 0.02123467 | -0.19758819 | 0.20288795 | -0.1592233 | -1.770231e-01 | 0.14720133 | 1.081542e-01 |
| **MinTe** | 0.33192281 | -0.4135757 | 0.42008014 | -0.35631005 | 0.35813423 | -0.2268466 | -3.176793e-01 | 0.21401587 | 2.670777e-01 |
| **MaxTe** | -0.26107635 | 0.3412123 | -0.19015946 | 0.42441025 | -0.43315089 | 0.5172708 | 4.797893e-01 | -0.11535980 | 7.276541e-02 |
| Time | -0.26441905 | 0.4125322 | -0.22918196 | 0.43397314 | -0.52018532 | 0.5684053 | 5.813386e-01 | -0.06495698 | 6.495698e-02 |

| | BG | T | M | Prey | RH | MinTe | MaxTe | Time |
|---|---|---|---|---|---|---|---|---|
| **PT** | 0.10455931 | 0.7881066 | -0.8084477 | -0.20190912 | 0.09600082 | 0.3319228 | -0.26107635 | -0.26441905 |
| NT | -0.29934217 | -0.9878783 | 0.9600769 | 0.50377764 | -0.21416656 | -0.4135757 | 0.34121235 | 0.41253223 |
| IT | 0.50706702 | 0.8119895 | -0.7798649 | -0.17371944 | 0.02123467 | 0.4200801 | -0.19015946 | -0.22918196 |
| S | -0.08141321 | -0.9716306 | 0.9789065 | 0.43735233 | -0.19758819 | -0.3563100 | 0.42441025 | 0.43397314 |
| LLP | -0.21733788 | 0.9282339 | -0.9577707 | -0.53421695 | 0.20288795 | 0.3581342 | -0.43315089 | -0.52018532 |
| **LLN** | 0.46353509 | -0.7907932 | 0.8447284 | 0.46168409 | -0.15922333 | -0.2268466 | 0.51727080 | 0.56840530 |
| G | 0.28800922 | -0.8800720 | 0.9061604 | 0.56231061 | -0.17702308 | -0.3176793 | 0.47978933 | 0.58133862 |
| L | 0.17282528 | 0.5703518 | -0.5942502 | -0.05283092 | 0.14720133 | 0.2140159 | -0.11535980 | -0.06495698 |
| **R** | 0.93325653 | 0.4436070 | -0.3445653 | -0.14209039 | 0.10815424 | 0.2670777 | 0.07276541 | 0.06495698 |
| BG | 1.00000000 | 0.1511425 | -0.0460862 | 0.03660778 | -0.05318322 | 0.2067012 | 0.19158010 | 0.21329796 |
| T | 0.15114253 | 1.0000000 | -0.9883135 | -0.52595397 | 0.21451635 | 0.4031822 | -0.38836317 | -0.46516239 |
| M | -0.04608620 | -0.9883135 | 1.0000000 | 0.50204326 | -0.22012914 | -0.4258937 | 0.36757835 | 0.44082649 |
| **Prey** | 0.03660778 | -0.5259540 | 0.5020433 | 1.00000000 | -0.52578205 | -0.0505981 | 0.44678320 | 0.41422430 |
| **RH** | -0.05318322 | 0.2145163 | -0.2201291 | -0.52578205 | 1.00000000 | -0.4831674 | -0.31137399 | -0.25989854 |
| **MinTe** | 0.20670122 | 0.4031822 | -0.4258937 | -0.05059810 | -0.48316738 | 1.0000000 | 0.47026801 | 0.21312301 |
| **MaxTe** | 0.19158010 | -0.3883632 | 0.3675783 | 0.44678320 | -0.31137399 | 0.4702680 | 1.00000000 | 0.79926014 |
| Time | 0.21329796 | -0.4651624 | 0.4408265 | 0.41422430 | -0.25989854 | 0.2131230 | 0.79926014 | 1.00000000 |

Table E.3. JNR redundancy analysis model results with variables that were retained following the step selections, where row 1,3,5,7 are fynbos sites and row 2,4,6,8 are pine forest sites.

```
Call:
rda(formula = dis ~ MaxTe + MinTe + Time + PT + P, data = env)

Partitioning of variance:
              Inertia Proportion
Total          0.5008    1.00000
Constrained    0.4806    0.95966
Unconstrained  0.0202    0.04034

Eigenvalues, and their contribution to the variance

Importance of components:
                          RDA1   RDA2    RDA3      RDA4      RDA5
Eigenvalue            0.3064 0.1615 0.01112 0.0008148 0.0006866
Proportion Explained  0.6119 0.3226 0.02220 0.0016300 0.0013700
Cumulative Proportion 0.6119 0.9345 0.95666 0.9582900 0.9596600
                          PC1      PC2
Eigenvalue            0.01694 0.003262
Proportion Explained  0.03383 0.006510
Cumulative Proportion 0.99349 1.000000

Accumulated constrained eigenvalues
Importance of components:
                          RDA1   RDA2    RDA3      RDA4      RDA5
Eigenvalue            0.3064 0.1615 0.01112 0.0008148 0.0006866
Proportion Explained  0.6376 0.3361 0.02314 0.0017000 0.0014300
Cumulative Proportion 0.6376 0.9737 0.99688 0.9985700 1.0000000

Scaling 2 for species and site scores
* Species are scaled proportional to eigenvalues
* Sites are unscaled: weighted dispersion equal on all dimensions
* General scaling constant of scores:  1.368337


Species scores

                     RDA1      RDA2     RDA3      RDA4      RDA5
A.atra          -0.66340 -0.451377  0.06534 -0.018614 -0.003407
A.porphyreus    -0.34648  0.526053 -0.04381 -0.029232 -0.004517
C.cordylus      -0.35107 -0.209421 -0.17843  0.004160  0.004831
T.seps          -0.02736 -0.015581 -0.02743  0.030696 -0.007248
T.capensis      -0.02445 -0.005492 -0.00844  0.002985 -0.049315
T.homalocephala  0.67891 -0.281710 -0.05219 -0.029611 -0.005205
                    PC1
A.atra          -0.07091
A.porphyreus    -0.07475
C.cordylus       0.13277
T.seps           0.02359
T.capensis       0.04402
T.homalocephala  0.18055


Site scores (weighted sums of species scores)

        RDA1     RDA2     RDA3      RDA4     RDA5        PC1
row1 -0.4844 -0.31493  1.49211  0.288754  0.30749 -0.659985
row2  0.6260 -0.06396 -0.01805 -0.023809 -0.03136  0.496116
row3 -0.4114 -0.19505 -0.26166 -1.113572  0.47323  0.002681
row4 -0.2690  1.27347  0.18339  0.100540  0.23643 -0.232585
row5 -0.3416 -0.24008 -0.77205 -0.006304 -1.56359  0.773100
row6  0.6260 -0.06396 -0.01805 -0.023809 -0.03136 -0.655460
row7 -0.3717 -0.33153 -0.58764  0.802009  0.64052 -0.050474
row8  0.6260 -0.06396 -0.01805 -0.023809 -0.03136  0.326608


Site constraints (linear combinations of constraining variables)

        RDA1     RDA2      RDA3     RDA4     RDA5        PC1
row1 -0.3887 -0.37849  0.894420  0.14634 -0.1495 -0.659985
row2  0.5246 -0.10027  0.524014  0.21463  0.1152  0.496116
row3 -0.4244 -0.23092 -0.219357 -1.05653  0.3904  0.002681
row4 -0.2445  1.22480  0.001757  0.09142  0.0138 -0.232585
row5 -0.4294 -0.09647 -0.148246  0.05243 -0.8662  0.773100
```

```
row6  0.7059 -0.17015 -0.564116 -0.09794 -0.5862 -0.655460
row7 -0.3670 -0.34385 -0.625118  0.80278  0.5881 -0.050474
row8  0.6235  0.09535  0.136646 -0.15313  0.4944  0.326608


Biplot scores for constraining variables

         RDA1     RDA2     RDA3   RDA4     RDA5 PC1
MaxTe  0.1063 -0.68862  0.51326 0.4391  0.24130   0
MinTe  0.2869 -0.04983  0.66318 0.4079  0.55587   0
Time  -0.6373 -0.14968  0.41332 0.6327 -0.01969   0
PT     0.8478  0.52247  0.06141 0.0119  0.06652   0
P     -0.8705 -0.13816 -0.12962 0.4413  0.10775   0
```

Table E.4. WMR redundancy analysis model results with variables that were retained following the step selections, where row 1, 5, 9, 13 are fynbos sites, row 2, 6, 10, 14 are semi-invaded sites, row 3, 7, 11, 15 are heavily-invaded sites and row 4, 8, 12, 16 are pine forest sites.

```
Call:
rda(formula = dis ~ MaxTe + MinTe + PT + LLN + RH, data = env)

Partitioning of variance:
              Inertia Proportion
Total          0.4181     1.0000
Constrained    0.2284     0.5462
Unconstrained  0.1897     0.4538

Eigenvalues, and their contribution to the variance

Importance of components:
                          RDA1    RDA2    RDA3     RDA4      RDA5
Eigenvalue            0.1315 0.07498 0.01623 0.005324 0.0003066
Proportion Explained  0.3145 0.17933 0.03882 0.012730 0.0007300
Cumulative Proportion 0.3145 0.49388 0.53270 0.545430 0.5461700
                          PC1    PC2     PC3     PC4      PC5
Eigenvalue            0.08303 0.0514 0.03629 0.01637 0.002651
Proportion Explained  0.19860 0.1229 0.08681 0.03916 0.006340
Cumulative Proportion 0.74476 0.8677 0.95450 0.99366 1.000000

Accumulated constrained eigenvalues
Importance of components:
                          RDA1    RDA2    RDA3     RDA4      RDA5
Eigenvalue            0.1315 0.07498 0.01623 0.005324 0.0003066
Proportion Explained  0.5759 0.32834 0.07108 0.023310 0.0013400
Cumulative Proportion 0.5759 0.90426 0.97534 0.998660 1.0000000

Scaling 2 for species and site scores
* Species are scaled proportional to eigenvalues
* Sites are unscaled: weighted dispersion equal on all dimensions
* General scaling constant of scores:  1.582496


Species scores

                     RDA1     RDA2      RDA3      RDA4       RDA5
A.atra          -0.03236 -0.06088 -0.132483  0.067265 -0.0111754
B.pumilum       -0.02288 -0.04305 -0.093680  0.047563 -0.0079022
C.cordylus      -0.02288 -0.04305 -0.093680  0.047563 -0.0079022
P.geitje        -0.02288 -0.04305 -0.093680  0.047563 -0.0079022
T.seps           0.37123 -0.10744  0.203900  0.093896 -0.0132255
T.tetradactylus  0.01693 -0.01881  0.009084 -0.098140 -0.0357524
T.homalocephala  0.57587 -0.42430 -0.084145 -0.046088  0.0084314
T.capensis      -0.56159 -0.49790  0.067862  0.002161  0.0004352
                       PC1
A.atra           0.0405005
B.pumilum        0.0286382
C.cordylus       0.0286382
P.geitje         0.0286382
T.seps          -0.6068391
T.tetradactylus -0.0027983
T.homalocephala -0.3535259
T.capensis       0.0007534


Site scores (weighted sums of species scores)

          RDA1      RDA2    RDA3      RDA4    RDA5         PC1
row1   0.15329 -0.558054  0.2069 -0.17761  1.4591  0.1129936
row2  -0.01109 -0.572341 -0.6083 -1.37518  4.4689  0.1437116
row3   0.65379  0.001945  0.5663  0.82591 -1.2618 -0.2914127
row4   0.14592 -0.356722  1.0946  1.15912 -2.0941 -0.4941815
row5   0.66794 -0.043960  0.3514  0.50856 -0.4145 -0.1968820
row6   0.53467 -0.105617 -1.1701 -1.67952  5.1745  0.0171494
row7  -0.19639  0.839165 -0.3046 -0.23422  0.5839  0.9382333
row8  -0.19639  0.839165 -0.3046 -0.23422  0.5839  0.4271927
row9   0.38503 -0.414577  0.2100 -0.00364  1.0166 -0.1533375
```

```
row10 -0.14426 -0.551159  0.4076 -1.02002 -5.1670 -0.0221604
row11  0.57727  0.159599  1.0789  1.59319 -3.3569 -0.9273416
row12 -0.90931 -0.269512  0.3934 -0.16646  0.8208  0.1972300
row13 -0.35837 -0.376750 -1.7054  1.43898 -3.8020  0.2378634
row14 -0.19639  0.839165 -0.3046 -0.23422  0.5839 -0.0000675
row15 -0.19639  0.839165 -0.3046 -0.23422  0.5839  0.1792860
row16 -0.90931 -0.269512  0.3934 -0.16646  0.8208 -0.1682768
```

Site constraints (linear combinations of constraining variables)

```
          RDA1    RDA2     RDA3     RDA4     RDA5        PC1
row1   0.22287 -0.7610 -0.15394  0.36152  0.36927  0.1129936
row2   0.02334 -0.3260 -0.07406 -0.33130  0.59230  0.1437116
row3   0.56144  0.1868  0.27306  0.02652  0.74179 -0.2914127
row4  -0.22975 -0.2966  0.80346  0.28007  0.37679 -0.4941815
row5   0.59792  0.0253 -0.16470  0.54911 -0.63389 -0.1968820
row6   0.28473  0.2323 -0.06387 -0.29085 -0.24071  0.0171494
row7   0.44679  0.3063  0.34434 -0.07911  0.02085  0.9382333
row8  -0.22423  0.3012  0.51327  0.37854 -0.36911  0.4271927
row9   0.22471 -0.5444 -0.14844 -0.05019 -0.48971 -0.1533375
row10  0.13409 -0.1489  0.07194 -0.77720 -0.28313 -0.0221604
row11  0.09748  0.4433 -0.04736 -0.22648 -0.27984 -0.9273416
row12 -0.70562 -0.2914  0.46902 -0.39201 -0.38782  0.1972300
row13 -0.19006 -0.3575 -0.77809  0.39505 -0.06563  0.2378634
row14 -0.43083  0.1519 -0.60358 -0.56695  0.27781 -0.0000675
row15 -0.03927  0.7885 -0.33312  0.13980  0.30685  0.1792860
row16 -0.77359  0.2902 -0.10794  0.58350  0.06420 -0.1682768
```

Biplot scores for constraining variables

```
         RDA1      RDA2    RDA3    RDA4     RDA5 PC1
MaxTe  0.3229 -0.444990 -0.1505 -0.1734  0.8031   0
MinTe -0.1452  0.151325  0.0944  0.4768  0.8484   0
PT    -0.4771  0.620080  0.5225 -0.2152  0.2618   0
LLN    0.6922 -0.117500 -0.6312 -0.3086  0.1158   0
RH     0.4387 -0.002633  0.7424 -0.1931 -0.4681   0
```

## Appendix F. Comparing lizard assemblages in fynbos (and pine forest) habitats between Jonkershoek Nature Reserve and Witzenberg Mountain Range

An ANOSIM of square-root transformed abundance data revealed that significant differences were apparent in lizard assemblages between locations of the fynbos habitat (global R = 0.967, P = 0.001, number of permutations = 999, Figure Fa) and in presence-absence data only (global R = 0.7, P = 0.001, number of permutations = 999, Figure Fb). Whereas, in the pine forest habitat there were no differences between locations for square-root transformed abundance data (global R = 0.034, P = 0.176, number of permutations = 999, Figure Fc) and presence-absence data only (global R = 0.031, P = 0.219, number of permutations = 999, Figure Fd).

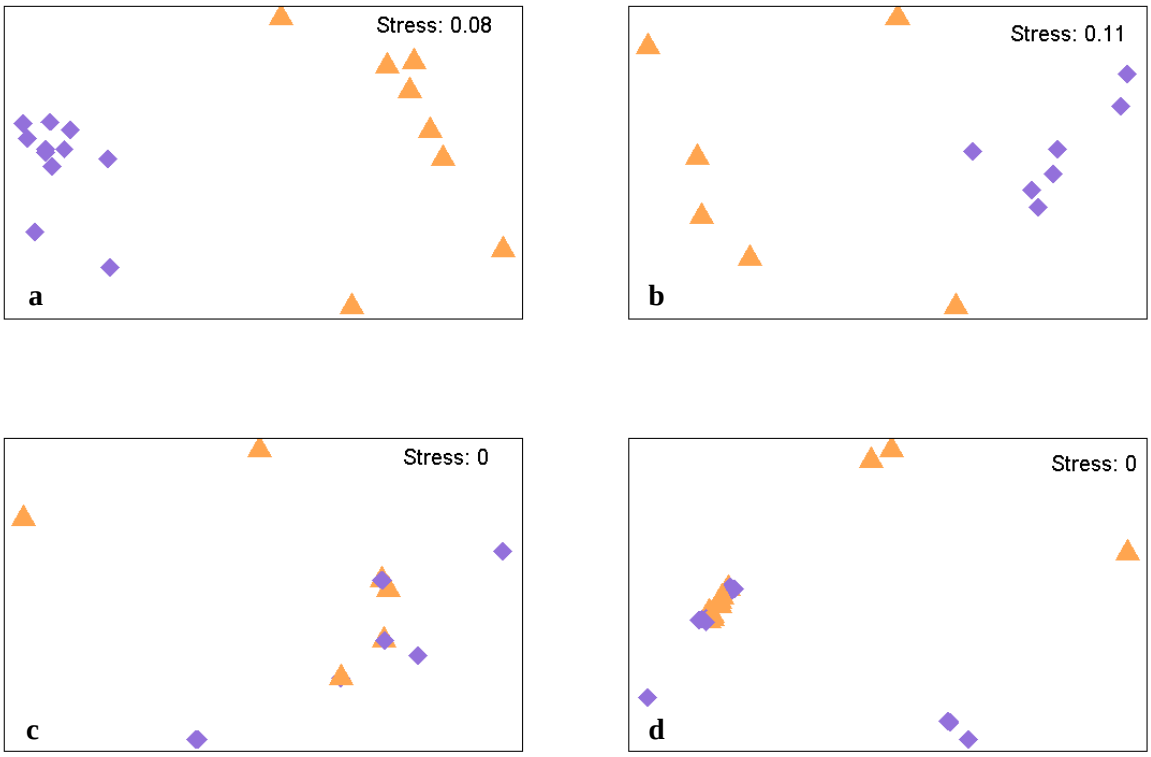


Figure F. NMDS ordination of Bray-Curtis similarities based on square-root-transformed lizard abundance data in fynbos (a) and pine forest (c), and presence/absence data in fynbos (b) and pine forest (d). Purple diamonds are samples from JNR and orange triangles are samples from WMR. Total of 11 samples (= surveys) per location. Due to similarity, some data are overlaid on top of one another.